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TOPOGRAPHY AND VASCULARIZATION OF BROWN FAT DEPOSITS IN THE LITTLE BROWN BAT, *MYOTIS LUCIFUGUS* AND THE DEER MOUSE, *PEROMYSCUS MANICULATUS*

by

© JOSEFINE CONSTANTIA RAUCH

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Topography and Vascularization of Brown Fat Deposits in the Little Brown bat, *Myotis lucifugus*, and the Deer Mouse, *Peromyscus maniculatus*" submitted by Josefine Constantia Rauch, in partial fulfilment for the degree of Master of Science.

ABSTRACT

The topography and vascularization of brown adipose tissue was investigated in a hibernator, the little brown bat *(Myotis lucifugus)*, and in a non-hibernator, the deer mouse *(Peromyscus maniculatus)* in an attempt to provide accurate information of the anatomical and vascular relations of brown adipose tissue in these species.

To locate the various brown fat deposits, regional dissections were performed in freshly-killed (non-preserved) and in preserved specimens. To outline the blood vessels that supply and drain brown fat deposits, regional dissections were performed on methacrylate-injected, preserved specimens.

Brown fat deposits were localized in four major body regions, the neck, external thorax, internal thorax, and internal abdomen. The tissue occupied the same, general body regions in both species. A close relationship was noted between the heart, the major anterior blood vessels, the sympathetic chain, the suprarenal glands, and brown adipose tissue. Two types of vascular arrangements of brown fat deposits were recognized. In the first type, a major artery, about which brown fat is deposited, provides branches to this tissue. The venous pattern, associated with such deposits, corresponds closely to that of the arterial system. The second type of vascular arrangement is peculiar to the interscapular brown adipose tissue and is different in the bat and deer mouse. In the former, the transverse cervical vessels have become specialized to provide the interscapular brown fat deposit with large blood channels. In the latter, a venous shunt system is associated

with the interscapular brown adipose tissue.

The distribution of brown adipose tissue and its relationship to the vascular system appears to be such that, during conditions of increased thermogenesis by brown fat, heat can be conveyed efficiently from this tissue to those structures whose functions are of vital importance for arousal from hibernation and for maintenance of thermal equilibrium during cold exposure.

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INTRODUCTION

The first detailed description of the anatomy of brown adipose tissue was given by Hammar (1895). He distinguished two types of mammalian adipose tissue from his work on the rat: "Weisses Fettgewebe" (white adipose tissue); and "Braunes Fettgewebe" (brown adipose tissue). He localized all brown fat deposits in the rat and recorded their occurrence in the following regions: between the scapulae (interscapular brown adipose tissue) and the muscles of the back; in various areas of the neck; in the axillary, inguinal, perianal, and mediastinal regions; to either side of the thoracic vertebrae; along the inferior vena cava, descending aorta, and internal mammary vessels; and between the kidneys, where renal and suprarenal vessels are embedded in brown fat. Also, Hammar claimed that the much reputed (review Auerbach, 1901/02) "hibernating gland" (interscapular brown fat deposit) is brown adipose tissue that can be identified, developmentally and structurally, with the brown fat of other deposits.

Attempts to identify the "hibernating gland" with brown adipose tissue were made at a still earlier date. Thus, Jacobson (1817) held that this "gland" comprised a modified form of fatty tissue. Ehrman (1883) not only rejected a glandular nature of the interscapular brown fat but refused also to accept that it occurs only in hibernators. He argued that the "hibernating gland" is not a discrete organ of a particular group of animals (hibernators), but adipose tissue, common at least to all mammals. Ehrman's argument was based partly on assumption since all mammals had not been investigated for the presence of brown adipose tissue.

Substantial evidence in recent literature (see reviews by Johansson, 1959 and Smalley and Dryer, 1967) has shown that brown fat is present in a variety of mammalian embryos, including those of most domesticated animals and man. Apparently it is retained throughout adult life in all "true" hibernators and in a variety of small non-hibernators.

Although much information about the anatomy, histology, and embryological development of brown adipose tissue has been available since the beginning of this century, the modern idea of the function of this tissue was not appreciated until recently when Smith (1962) proposed a high thermogenic capacity for brown fat. His supposition was based on a high *in vitro* oxygen consumption of brown adipose tissue from cold-acclimated rats. Smith and Hock (1963) demonstrated that the temperature adjacent to brown fat deposits is higher and increases at a faster rate than that of the deep rectal area in the marmot arousing from hibernation. These findings have been substantiated by later studies which show that brown adipose tissue is a major site of heat production during arousal from hibernation (Smith and Hock, 1963; Smalley and Dryer, 1963; Joel, Treble, and Ball, 1964; Hayward, Lyman, and Taylor, 1965; Chaffee *et al.*, 1966; Hayward and Ball, 1966; Hayward and Lyman, 1967; Horwitz, Smith, and Pengelley, 1968), during cold-acclimation (Cameron and Smith, 1964; Chaffee *et al.*, 1964; Smith and Roberts, 1964), cold stress (Donhoffer and Szelényi, 1967), and early post-natal life (Dawkins and Hull, 1964; Dawkins and Scopes, 1965; Silverman *et al.*, 1964; Brück and Wünnenberg, 1966; Hull and Segall, 1965a, 1965b, 1965c).

Further evidence, confirming a high thermogenic potential for brown fat, has been obtained from biochemical studies. There is substantial evidence that triglyceride catabolism and fatty acid re-esterification may occur in brown adipose tissue (Dawkins and Hull, 1964; review Smalley and Dryer, 1967). Both reactions are believed to contain energetically inefficient steps (Ball and Jungas, 1961; Masoro, 1963; Joel, Neaves, and Rabb, 1967), the consequence of which is relatively large amounts of heat production. Such reactions, initiated by an appropriate stimulus (review Smalley and Dryer, 1967) could account for the high thermogenic role of brown adipose tissue during arousal from hibernation, cold-acclimation, and cold stress. The high mitochondrial content of brown adipose tissue (Lever, 1957; Napolitano and Fawcett, 1958; review Remillard, 1958; Hayward and Lyman, 1967) is held generally to verify (on an ultrastructural basis) the capacity of the tissue for high rates of metabolism.

Several workers (Johansen, 1961; Bullard and Funkhauser, 1962; Heim and Hull, 1966; Kuroshima, Konno, and Itoh, 1967; Rauch, unpubl. data) have utilized regional blood flow studies as an index for the high metabolic capacity of brown fat. All findings have revealed that there is a highly significant increase of blood flow through brown adipose tissue during arousal from hibernation, cold-acclimation, and cold stress.

A functional association between the anatomical disposition and the thermogenic role of brown fat was presented by Smith and Roberts (1964). They deduced that the close proximity of brown fat to structures such as the heart and sympathetic chain would permit an efficient heat transfer to these central structures.

Because of the vascular arrangement of the interscapular brown fat deposit in the rat, Smith and Roberts (1964) proposed a regulated, counter-current heat exchange mechanism for the circulation to interscapular brown fat. This system, in conjunction with a venous shunt, could control the temperature of the arterial blood supply to the interscapular brown adipose tissue. An elevated temperature of the arterial blood would increase the metabolic rate of the tissue and, therefore, its heat production. A lowered temperature would have the opposite effect.

Despite the voluminous literature on brown adipose tissue, only fragmentary information (Smith and Roberts, 1964; Hull and Segall, 1965a) is available on the gross anatomy of the blood vessels supplying and draining brown fat deposits in non-hibernators. Such information should prove valuable in supplementary experimentation, particularly concerning the dynamics of blood flow through brown fat. Furthermore, except for the interscapular brown fat deposit and its vascularization in the bat (Krutzsch and Sulkin, 1959), a detailed description of brown fat and its relationship to the circulatory system is not known in any species capable of hibernation. According to Smalley and Dryer (1967), such information is critically needed.

An attempt is made, therefore, to present a detailed description of the distribution of brown fat and the gross anatomy of the blood vessels supplying and draining all brown fat deposits in a hibernator (the little brown bat, *Myotis lucifugus lucifugus*, Le Conte) and in a non-hibernator (the deer mouse, *Peromyscus maniculatus borealis*, Mearns).

MATERIALS AND METHODS

A. ANIMALS

Bats

Roosting bats were collected by hand from under the roofs of old houses adjacent to Lake Wabamun (53°30' North; 114°35' West). Large colonies of bats were found in this region during summer and collecting was done during the last week of July, 1967. Bats were transported to the University of Alberta in large wire cages. Several bats were obtained in September, 1967, during their migration through Edmonton. They were caught by hand in local buildings.

The bats were divided into three groups, as indicated in Table I. Group 1 consisted of 10 animals. They were retained in a wire cage and kept at room temperature (25°C - 27°C) for two to four weeks before being used in study. Group 2 consisted of 10 animals. They were placed individually in glass jars with wire mesh lids so that the removal of one would not disturb the others during hibernation. A rectangular piece of wire mesh was placed inside each jar. This allowed the bats to assume their usual, hanging position. Hibernation was induced in these animals by placing them into a cold room at 2°C. They were kept in hibernation for two to three weeks before being used in study. Group 3 consisted of 20 animals, 10 from the Lake Wabamun area, and 10 from Edmonton (53°35' North; 113°30' West). The bats from the Lake Wabamun area were retained in a large wire cage. The bats from Edmonton were placed individually (since they were obtained individually) into glass jars. The group 3 bats were kept at room temperature (25°C - 27°C) and used for studies within a day or two

Table I. Summary of the samples of bats and deer mice investigated for the topography, arterial supply, and venous drainage of brown adipose tissue (B.A.T.).

Species	Group	No. of Animals	Month of Capture	Area of Capture	Time in Captivity -days-	Temperature	Investigation
Myotis lucifugus lucifugus	1	10	July 1967	Wabamun	14 - 30	25°C - 27°C	Topography of B.A.T. (freshly killed specimens)
	2	10	July 1967	Wabamun	14 - 21	2°C - 3°C	
	3	5	Sept. 1967	Edmonton	0 - 2	25°C - 27°C	
	3	10	July 1967	Wabamun	0 - 2	25°C - 27°C	Circulation and Topography of B.A.T. (preserved specimens)
	3	5	Sept. 1967	Edmonton	0 - 2	25°C - 27°C	
Peromyscus maniculatus borealis	1	10	May to July 1967	Edmonton	30 - 60	25°C - 27°C	Topography of B.A.T. (freshly killed specimens)
	1	10	Sept. 1967	Grande Prairie	30 - 90	25°C - 27°C	
	2	20	Sept. 1967	Grande Prairie	30 - 90	2°C - 4°C	
	3	35	Sept.-Nov. 1966; May-June 1967	Edmonton	0 - 2	23°C - 27°C	Circulation and Topography of B.A.T. (preserved specimens)
	3	5	Sept. 1967	Grande Prairie	30 - 90	2°C - 4°C	

of the time of capture.

Except for those in hibernation, all bats had free access to water and were fed mealworms once a day.

Deer mice

Deer mice were caught with live traps in forests near Edmonton and Grande Prairie (55°10'North; 118°48'West), Alberta. The Grande Prairie region was chosen as a secondary collecting area because the low density of *P. maniculatus borealis* close to Edmonton during 1967 made it difficult to obtain the required number of animals locally.

The deer mice were kept in groups of 2 or 3 individuals. Water and food (Vita-Mite Cubes) were provided *ad libitum*.

The animals were arranged as shown in Table I. Group 1, consisting of 20 animals, was warm-acclimated. These animals were maintained at room temperature (25°C - 27°C) for one to three months before use in study. Group 2 consisted of 20 animals. They were cold-acclimated at 2°C - 4°C, and maintained at this temperature for up to three months before use in study. Group 3 was comprised of 40 animals. Thirty-five of them were kept at room temperature (23°C - 27°C) for up to two days before use in study. The remaining 5 animals were kept at a temperature of 2°C - 4°C for up to three months before use in study.

The arrangement of bats and deer mice into various groups, and their subsequent exposure to differing environmental conditions, is not a major objective of the present investigation. A concurrent blood flow study required that a group of bats be induced to hibernate and a control group kept at room temperature. For the

same purpose, deer mice were warm- and cold-acclimated. Therefore, this anatomical study was conducted as a prerequisite to interpretation of blood flow results. The blood flow study will not be included in this thesis.

B. METHODS OF KILLING

All animals investigated merely for the topography of brown adipose tissue (Table I) were killed by an intravenous injection of saturated KCl (10 cc/kg body weight). Rapid killing, as achieved by this method, was required because of the aforementioned, concurrent blood flow study in these animals. They consisted of group 1, 2, and some of the group 3 bats; of group 1 and 2 deer mice. Regional dissections were performed on these animals immediately following death.

The majority of group 3 bats and the entire group 3 deer mice were killed with excess Pentobarbital Sodium (150 mg/kg body weight) injected intraperitoneally. No blood flow studies were performed in these animals. They were investigated for the relationship between blood vessels and brown adipose tissue deposits. Consequently, their circulatory system was injected with methacrylate and the injected specimens were preserved.

C. METHOD OF INJECTING AND PRESERVATION

A longitudinal incision was made on each side of the sternum. These extended from the diaphragm to the level of the second rib. A third cut, across the xiphoid process, extended from the posterior corner of one longitudinal incision to the next. The semi-isolated flap of tissue was reflected anteriorly so as to reveal the internal mammary vessels. The cut end of these

vessels was ligated to prevent possible outflow of the material to be injected. A PE-20 polyethylene catheter was manipulated into the proximal aorta via a puncture in the left ventricle of the heart. The catheter was tied firmly into the vessel. Most of this procedure required the use of a dissecting microscope.

"Batson's No. 17 Anatomical Corrosion Compound"[1], a methyl methacrylate monomer, was injected through the polyethylene catheter. Simultaneously, the contents of the circulatory system were allowed to drain through a puncture in the right ventricle of the heart.

The ingredients of "Batson's No. 17 Anatomical Corrosion Compound" were mixed as follows: 2.5 ml of the base solution A was thoroughly mixed with 0.6 ml of the catalyst B and a small amount of the blue pigment provided. Another 2.5 ml of the base solution A was mixed with 3 drops of the promoter C in a separate glass dish. This separation was necessary since the combination of catalyst B and promoter C (also a catalyst) induces the polymerization of base A and thus rapid solidification of the liquid plastic. The two fluids were mixed together immediately prior to injection.

Methacrylate has several advantages over other injection media such as hot wax, vinylite, or latex. It is characterized by undergoing a minimum amount of shrinkage, good tensile strength, and can be used at room temperature. Furthermore, it appears to pass readily through the capillary beds, thereby filling both the arterial and venous portions of the circulation from one arterial injection.

Methacrylate-injected specimens were preserved in embalming fluid, as supplied by the Department of Anatomy, Faculty of

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[1]Polysciences Inc., Rydal, Pennsylvania.

Medicine, University of Alberta. Small amounts of embalming fluid were injected subcutaneously, intramuscularly, and intra-abdominally, at various sites in order to hasten the preservation process. The specimens were then completely immersed and maintained in embalming fluid for later dissections.

D. LOCALIZATION OF BROWN ADIPOSE TISSUE DEPOSITS

A total of 25 freshly-killed bats (groups 1, 2, and some of group 3) and 40 deer mice (groups 1 and 2) were investigated for the topography of brown fat. Regional dissections were performed under a dissecting microscope. Brown adipose tissue was identified by its reddish-brown colour and by its lobular structure. The various brown fat deposits were localized by removing successive muscle layers and viscera. Attention was given to possible observable differences in brown fat between animals maintained under different environmental conditions.

E. LOCALIZATION OF BLOOD VESSELS IN RELATION TO BROWN ADIPOSE TISSUE

A total of 15 methacrylate-injected, preserved bats (the majority of group 3 bats) and 40 deer mice (group 3) were investigated for the relationship between blood vessels and brown adipose tissue deposits. Regional dissections were performed as described above. In addition, the arteries passing through brown fat, or terminating in it, were traced to their origin from the major vessels of the heart. Similarly, the veins passing through brown fat, or originating in it, were followed to their entry into major veins. Standard anatomy textbooks (Gray, 1924; Grant, 1945;

Lockhart, Hamilton, and Fyfe, 1959; Greene, 1959) were used for the identification of the larger blood vessels from which those serving brown adipose tissue derived. Drawings were made concurrently with dissections.

RESULTS

A. GENERAL OBSERVATIONS

The distribution of brown adipose tissue (hereafter referred to as B.A.T.) in *M. lucifugus* and *P. maniculatus* is summarized in Table II. In these animals, brown fat is confined to the external thorax, neck region, internal thorax, and abdomen. The deposits within these general areas correspond closely to those in the rat (Hammar, 1895; Cameron and Smith, 1964) except that brown fat is absent from the inguinal and perianal regions of the bat and deer mouse.

The location of individual brown fat deposits was found to be identical in all bats investigated. Similarly, no variation in the position of this tissue was observed in the deer mouse.

Brown adipose tissue occupied a larger area in the bats collected during September than in those captured during July. In the former, adjacent deposits were continuous with each other. Large amounts of subcutaneous white fat were found in the abdominal region, and also surrounding both jugular and interscapular B.A.T. White fat was dispersed also between the muscles of the hind appendages. Discrete deposits of brown fat were present in the animals captured during July. These animals lacked subcutaneous white fat but small amounts of this tissue were distributed between the muscles of the legs.

Brown fat deposits occupied a smaller area in the bats which were killed during arousal from hibernation than in those which were kept at a room temperature of 25°C to 27°C. Inter-muscular white fat was present in the non-hibernating bats. It

Table II. An outline of the brown adipose tissue (B.A.T.) deposits in the little brown bat, *Myotis lucifugus lucifugus*, and the deer mouse, *Peromyscus maniculatus borealis*, according to the four major body regions.

Myotis lucifugus lucifugus

1. External Thoracic Brown Adipose Tissue
   Interscapular B.A.T.
   Clavo-scapular B.A.T.
   Subscapular B.A.T.
2. Neck Region Brown Adipose Tissue
   Squamo-occipito-cervical B.A.T.
   Jugular B.A.T.
   Carotid B.A.T.
   Basi-occipito-cervical B.A.T.
3. Internal Thoracic Brown Adipose Tissue
   Pericardial B.A.T.
   Inferior vena caval B.A.T.
   Aortic B.A.T.
   Intercostal B.A.T.
4. Abdominal Brown Adipose Tissue
   Inferior vena caval B.A.T.
   Aortic B.A.T.
   Renal B.A.T.
   Suprarenal B.A.T.

Peromyscus maniculatus borealis

1. External Thoracic Brown Adipose Tissue
   Interscapular B.A.T.
   Subscapular B.A.T.
   Axillary B.A.T.
2. Neck Region Brown Adipose Tissue
   Transverse cervical B.A.T.
   Squamo-occipito-cervical B.A.T.
   Jugular B.A.T.
   Carotid B.A.T.
3. Internal Thoracic Brown Adipose Tissue
   Pericardial B.A.T.
   Inferior vena caval B.A.T.
   Aortic B.A.T.
   Intercostal B.A.T.
4. Abdominal Brown Adipose Tissue
   Inferior vena caval B.A.T.
   Aortic B.A.T.
   Renal B.A.T.
   Suprarenal B.A.T.

was absent in the hibernating ones.

A distinct difference in the size of brown fat deposits was observed between the deer mice captured during late spring or early summer and those collected in autumn. In the former, discrete brown fat deposits were present; in the latter, adjacent deposits were continuous with each other. White fat was found under the integument, between the muscles of the legs, and surrounding superficially-located brown fat deposits.

There was no observable difference in the size of brown fat deposits between warm-acclimated and cold-acclimated deer mice. Both groups of animals were collected in autumn and had extensive brown fat deposits. Little or no white fat was detected in the cold-acclimated deer mice.

B. TOPOGRAPHY AND VASCULARIZATION OF BROWN FAT DEPOSITS

Figures 1 to 50 illustrate the brown fat deposits and their relations to adjacent structures in *M. lucifugus* and *P. maniculatus*. Special emphasis is given to the blood vascular system. The name-designation of a particular deposit denotes its relative location. Because of the seasonal changes in the mass of brown adipose tissue, some of the labelled deposits cannot be considered distinct entities. This is true particularly for the intrathoracic and abdominal brown adipose tissue. When a maximum amount of brown fat is present in late autumn, two or more brown fat deposits may merge; when the mass of brown fat declines to a minimum in early summer, the same deposits are discontinuous. Any such observation is included in the description of particular deposits, and the drawings represent what is believed to be an

average between the extreme seasonal amounts of brown adipose tissue. In parallel fashion, changes in the mass of brown fat are accompanied by corresponding changes in vascularization. Size and/or number of blood vessels increase as a given deposit enlarges; they decrease as brown adipose tissue declines in mass. Therefore, only the most frequently occurring blood vessels are presented in the drawings.

Since there is a close resemblance of the carotid B.A.T. in the two species, this deposit is drawn for the bat only. Also, the intrathoracic and abdominal brown fat deposits are very similar in the two species and are delineated for the deer mouse only.

Throughout the text, reference is made to the anatomy of man and rat, since the mammalian anatomy is known best in these species. For each brown adipose tissue deposit in the bat and deer mouse, a description of the localization of the tissue is presented first and then followed by details regarding the arterial and venous circulation.

Bats

1. External Thoracic Brown Adipose Tissue

a) Interscapular B.A.T.

The interscapular B.A.T. (Figs. 1, 2) is the largest of all brown fat deposits in the bat. It is a bilobed structure, located between the scapulae. The lobes extend from the back of the skull to the posterior third of the thorax. Their medial borders are in close proximity in the mid-dorsal line of the animal. An anterior extension of each lobe occupies a lateral position, filling the space between the skull and the superior boundary of the scapula. The lateral border of each extension is in contact

with the parotid gland, a superficial lymph node, and the jugular brown fat deposit (Fig. 2). The interscapular brown adipose tissue fills the cervico-dorsal fossa cranially and the interscapular depression caudally. It overlies part of the *Semispinalis capitis* and most of the *Trapezius*.

The gross anatomy of the interscapular B.A.T. in the little brown bat closely resembles that of other species of bats (Dalquest and Werner, 1951; Krutzsch and Sulkin, 1959).

Arterial supply. The interscapular B.A.T. is supplied by the transverse cervical artery (Figs. 2, 3, 4, 5, 6, 13, 14, 18), which is the larger of the two terminal branches of the cervical arterial trunk (Figs. 14, 18, 20). This trunk corresponds to the thyrocervical arterial trunk in man and the deer mouse (Figs. 41, 48, 50). The transverse cervical artery provides a branch to the clavo-scapular B.A.T. (Fig. 4) close to its origin. Another branch supplies the *Trapezius* immediately before the artery enters the anterior extension of the interscapular B.A.T. At this point, the vessel divides into two or three smaller arteries. Multitudinous arterioles branch from these arteries as they course toward their termination, close to the posterior border of the interscapular brown fat deposit.

The transverse cervical artery of the bat is anatomically and functionally distinct from that of the deer mouse (Fig. 24), rat, and man. It does not supply any branches to the muscles of the neck and upper back except the aforementioned artery to the *Trapezius*. Its relative size is much larger in the bat than in other animals, in which the interscapular B.A.T. is not supplied by the transverse cervical artery. These findings suggest that,

in the bat, the primary purpose of this artery is to provide a very large blood channel to the interscapular brown fat deposit.

Krutzsch and Sulkin (1959) indicated that the interscapular brown fat in the insectivorous bats, *Pipistrellus subflavus* and *Myotis lucifugus,* is supplied by branches which correspond to the transverse cervical arteries in man. Their description corresponds to the present finding but their illustration does not. It appears as if Krutzsch and Sulkin labelled the common carotid artery as internal carotid artery, and the cervical arterial trunk as external carotid artery. Their drawing does not indicate the presence of a common carotid artery, nor of a cervical arterial trunk, and it represents the transverse cervical artery as a branch of the external carotid artery.

Venous drainage. The interscapular B.A.T. is drained by the transverse cervical vein (Figs. 2, 3, 4, 5, 6, 13, 19, 20). This vessel corresponds closely to the transverse cervical artery. It receives a small tributary from the *Trapezius* and the clavo-scapular B.A.T. (Fig. 4), and is joined by the transverse scapular vein (Figs. 4, 5, 13, 19) close to its termination at the external jugular vein (Figs. 13, 19).

In man, the transverse scapular vessels have been termed recently the suprascapular vessels (Huelke, 1958).

b) Clavo-scapular B.A.T.

The clavo-scapular brown fat deposit (Figs. 3, 4) fills the cone-shaped fossa between the distal third of the clavicle and the *Subclavius* ventrally, the lateral portion of the scapula dorsally, and the upper thoracic cage medially. Within the deep aspect of this fossa, the axillary vessels and the brachial plexus

are embedded in brown fat. More superficially, the brown fat surrounds the transverse scapular vessels.

These findings are peculiar to the bat and likely a consequence of the evolutionary adaptation to flight. The semi-curved clavicle in the bat results in a pronounced clavo-scapular fossa. The axilloid is shallow and taken up by the membrane of the wing. Brachial nerves and axillary vessels are displaced dorsally and thus traverse the clavo-scapular fossa.

The clavo-scapular brown adipose tissue is continuous with the jugular B.A.T. (Figs. 9, 10) ventrally and the subscapular B.A.T. (Fig. 5) dorsally, when large amounts of brown fat are present.

Arterial supply. The clavo-scapular B.A.T. is supplied by a branch (Fig. 4) of the transverse cervical artery (Figs. 2, 3, 4, 5, 6, 18, 20), and a branch (Fig. 4) of the subscapular artery (Figs. 4, 5, 6, 14, 18, 20).

Venous drainage. The veins draining the clavo-scapular B.A.T. consist of a tributary (Fig. 4) of the transverse cervical vein (Figs. 4, 5, 13, 14) and a tributary (Fig. 4) of the subscapular vein (Figs. 4, 5, 6, 19, 20).

c) Subscapular B.A.T.

The subscapular B.A.T. is a flat lobe of brown adipose tissue (Fig. 5) situated between the scapula and the thoracic cage. Its ventral surface overlies the *Serratus anterior superior* and some external intercostal muscles; its dorsal surface is in close contact with the *Subscapularis*. The brown fat deposit envelopes that portion of the subscapular vessels (Fig. 6) which lies superficially to the *Subscapularis*.

The subscapular brown fat is continuous with the clavo-scapular brown fat when the mass of this tissue is large.

Arterial supply. The subscapular B.A.T. is supplied by at least three branches (Fig. 6) of the subscapular artery (Figs. 4, 5, 6, 14, 18, 20).

Venous drainage. The subscapular B.A.T. is drained by three or more tributaries (Fig. 6) of the subscapular vein (Figs. 4, 5, 6, 19, 20).

2. Neck Region Brown Adipose Tissue

a) Squamo-occipito-cervical B.A.T.

This triangular-shaped brown fat deposit (Figs. 7, 8) is situated near the mid-dorsal line, in the deep aspect of the upper neck region. It is covered dorsally by the *Semispinalis capitis*, and makes contact with the *Rectus capitis*, *Obliquus capitis*, and the cranial portion of the cervical spine ventrally. When large, this deposit extends between adjacent muscles, overlies the posterior part of the foramen magnum, and makes contact with the occipital bone of the skull. Its cranio-lateral border may extend to the mastoid process. The squamo-occipito-cervical B.A.T. surrounds the deep cervical or *Profunda cervicalis* artery (Fig. 8) and corresponding vein. Frequently it covers also the cervical plexus of spinal nerves.

Arterial supply. The squamo-occipito-cervical B.A.T. is supplied by several branches of the *Profunda cervicalis* (Fig. 8), which arises from the costocervical trunk (Fig. 18) of the sub-clavian artery.

Venous drainage. The squamo-occipito-cervical B.A.T. is drained by branches of the posterior tributary (Fig. 8) of the superior intercostal vein (Figs. 19, 20).

b) Jugular B.A.T.

The jugular B.A.T. lies in the ventral neck region, where it surrounds the external jugular vein (Figs. 11, 12, 13, 19, 20). It extends from the mid-ventral line of the animal to the lateral border of the neck. Here, it contacts the lateral extension of the interscapular B.A.T., but is separated from it by connective tissue. The jugular B.A.T. is continuous with the clavo-scapular B.A.T. when these deposits are large. The deep aspect of the jugular B.A.T. surrounds the proximal portion of the transverse cervical vessels (Fig. 13), and occasionally also the superficial cervical vessels (Figs. 14, 18).

Arterial supply. The jugular B.A.T. is supplied by at least two branches (Figs. 11, 18) of the superior thoracic artery (Figs. 12, 18, 20) and by two or three branches (Figs. 14, 18) of the superficial cervical artery.

The superior thoracic artery is a large vessel in the bat. It arises from either the superficial cervical artery, or from the cervical arterial trunk. This differs from the situation in man, where the small superior thoracic artery arises from the axillary artery. The large size of this vessel in the bat may be correlated with the large pectoral muscles, whose medial aspect it supplies.

Venous drainage. The medial half of the jugular B.A.T. is drained by at least two tributaries (Fig. 11) of the superior thoracic vein (Figs. 12, 19); the lateral half by a tributary (Fig. 11) of the posterior external jugular vein (Figs. 12, 19, 20), and a tributary (Fig. 11) of the external jugular vein (Figs. 11, 12, 13, 19, 20).

c) Carotid B.A.T.

The carotid B.A.T. (Fig. 11) lies in the ventral neck region. It occupies the space bordered medially by the *Sternohyoideus*, cranio-laterally by the posterior belly of the *Digastricus*, and caudo-laterally by the *Sternomastoideus* (Fig. 15). Within this space, the brown fat deposit surrounds the common carotid artery (Figs. 12, 13, 14, 20), internal jugular vein (Figs. 12, 13, 15, 17, 19), thyroid vessels, hypoglossal nerve, vagus nerve, a lymph node, and occasionally, the thyroid gland.

Arterial supply. The carotid brown fat is supplied by a branch (Figs. 12, 13, 14) of the common carotid artery (Figs. 12, 13, 14, 20). Occasionally, this vessel may arise from the occipital artery.

Venous drainage. The carotid brown fat is drained by a tributary (Figs. 12, 13) of the internal jugular vein (Figs. 12, 13, 15, 17, 19,20). No variations were observed.

d) Basi-occipito-cervical B.A.T.

This brown fat deposit (Fig. 16) lies dorsally to the trachea and oesophagus in the proximal aspect of the ventral neck region. The dorsal surface of this bilobed structure makes contact with the base of the skull cranially, and the proximal cervical spine caudally. Thus the foramen magnum is surrounded ventrally by brown adipose tissue. Laterally, this tissue may cover the medial aspect of the tympanic bulla as well as the carotid and jugular canal. The internal carotid artery, internal jugular vein, vagus nerve, hypoglossal nerve, and the sympathetic trunk are embedded frequently in this tissue.

Arterial supply. The artery supplying the basi-occipito-cervical B.A.T. may arise from the vertebral artery, as shown in Figure 17, or from the internal carotid artery.

Venous drainage. The vein draining the basi-occipito-cervical B.A.T. empties into a venous plexus close to the base of the skull (Fig. 17). The plexus consists of vessels draining spinal muscles, the upper pharynx and the basi-occipito-cervical B.A.T. It terminates in two communicating veins which are tributaries of the internal maxillary vein.

3. Internal Thoracic Brown Adipose Tissue

The intrathoracic brown adipose tissue is dispersed over a wide area. It overlies the heart, venae cavae, dorsal aorta, and it fills the intercostal spaces to each side of the vertebral column. Seemingly distinct deposits are associated with a small mass of brown fat in the early summer; a continuous sheath of brown adipose tissue exists in late fall when the mass of this tissue is large.

In the anterior thoracic cavity, the pericardial portion of the intrathoracic B.A.T. is situated in the upper mediastinum. It extends along the internal mammary vessels ventrally, and over the base of the heart dorsally. As the brown fat spreads behind the heart, it encloses the vagus nerve, phrenic nerve, and all the blood vessels close to the heart. Brown adipose tissue extends over the entire course of the inferior vena cava and dorsal aorta. In the posterior thoracic cavity, brown fat is found in the intercostal spaces. The spread of the intercostal B.A.T. varies greatly. It is almost absent during the early summer; it passes over the

azygos vein to become continuous with that of the dorsal aorta in late autumn. The intercostal B.A.T. covers the sympathetic trunk, splanchnic nerve, and that part of the intercostal vessels which lies close to the vertebral spine.

Arterial supply. The intrathoracic brown fat is supplied by a branch of the pericardial artery in the mediastinal region and by a number of small branches of the phrenic artery in the inferior vena caval region. Several branches of the dorsal aorta supply the remainder of the internal thoracic B.A.T.

Venous drainage. The internal thoracic B.A.T. is drained by tributaries of the pericardial vein, venae cavae, and azygos vein.

4. Abdominal Brown Adipose Tissue

The abdominal brown adipose tissue is a continuation of the intrathoracic brown fat. It extends into the abdomen through the openings in the diaphragm for the aorta and inferior vena cava. Within the abdomen, brown adipose tissue encloses the anterior half of the inferior vena cava and the abdominal aorta. The tissue spreads between the hila of the kidneys, where it surrounds the renal vessels. The suprarenal glands are enclosed completely in brown fat when this tissue is present in large amounts.

Arterial supply. The abdominal brown fat is supplied by small branches of the abdominal aorta, renal, and suprarenal arteries.

Venous drainage. The abdominal brown fat is drained by small tributaries of the inferior vena cava, renal, and suprarenal veins.

Fig. 1. Dorsal view of the interscapular brown adipose tissue (B.A.T.) deposit of *Myotis lucifugus*.

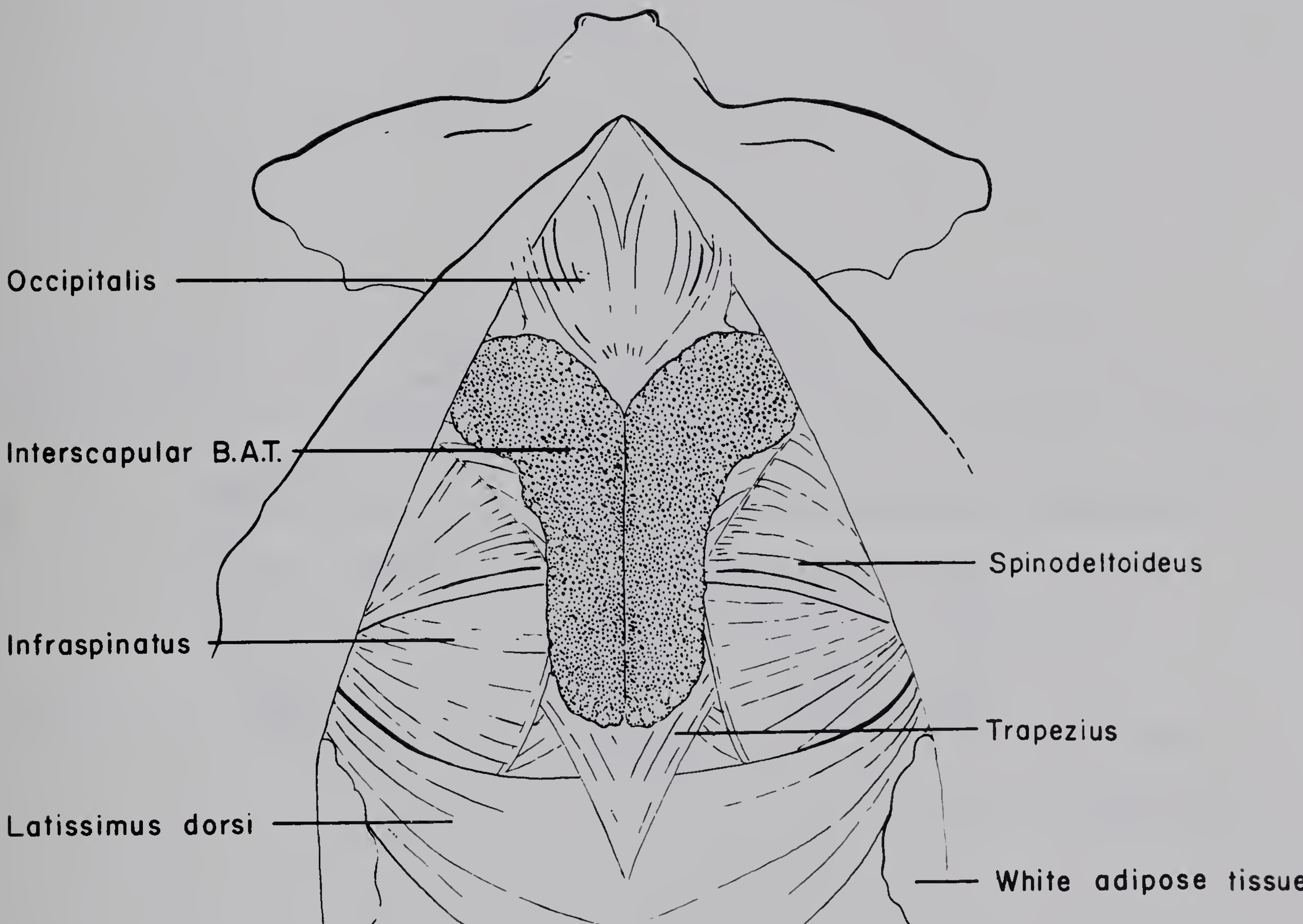
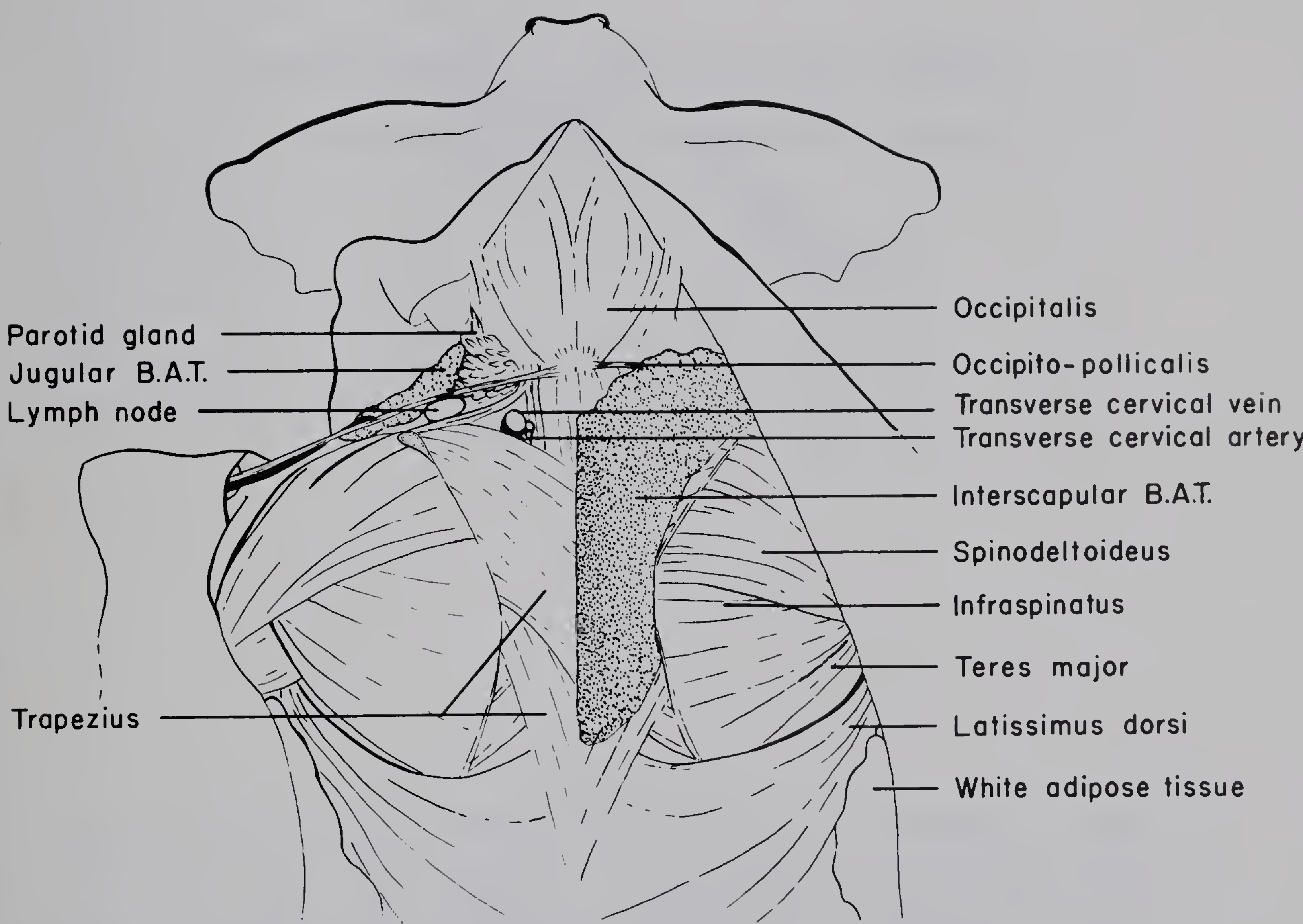

Occipitalis
Interscapular B.A.T.
Spinodeltoideus
Infraspinatus
Trapezius
Latissimus dorsi
White adipose tissue

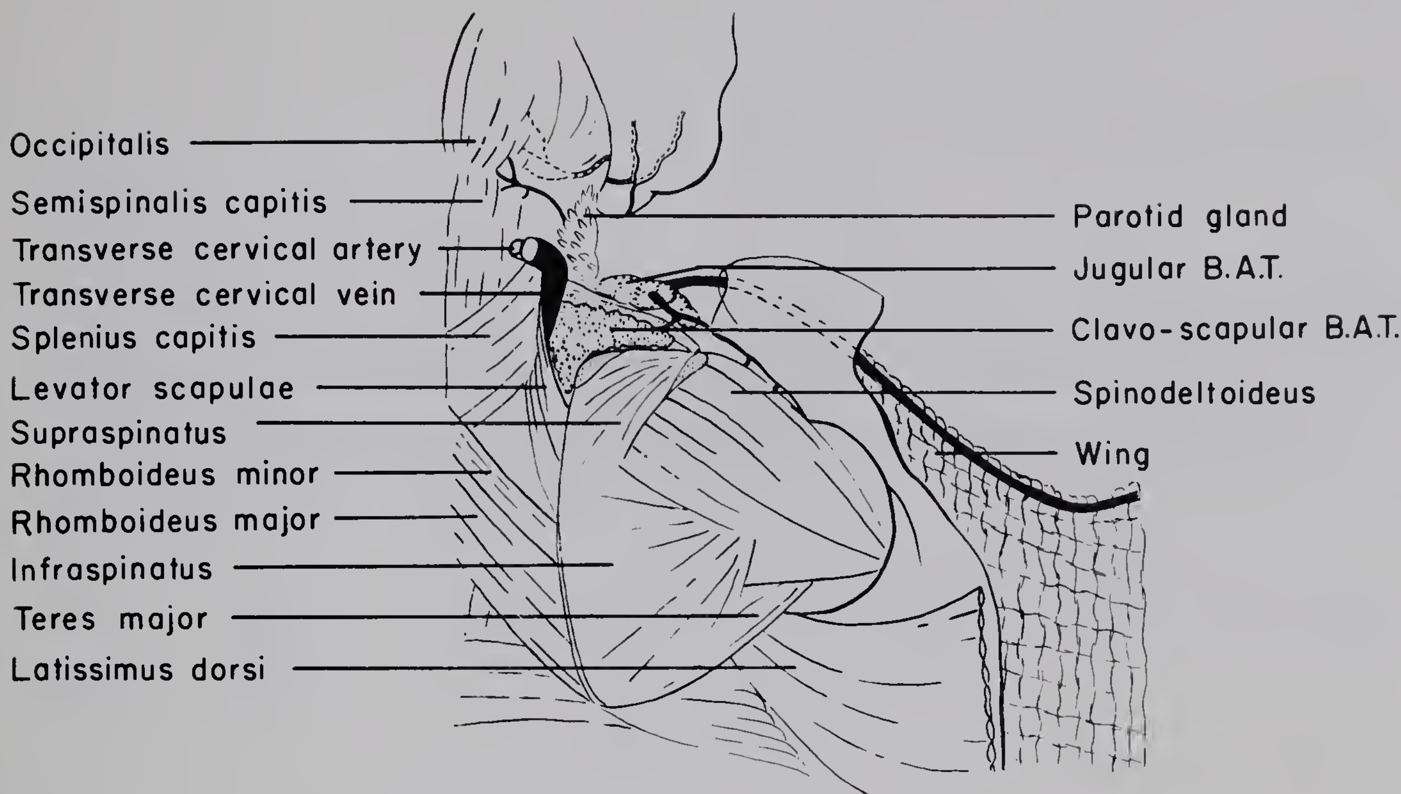
Fig. 2. Dorsal view of the right lobe of the interscapular brown adipose tissue of *Myotis lucifugus*. The cut ends of the left transverse cervical vessels are demonstrated.



Parotid gland
Jugular B.A.T.
Lymph node
Trapezius
Occipitalis
Occipito-pollicalis
Transverse cervical vein
Transverse cervical artery
Interscapular B.A.T.
Spinodeltoideus
Infraspinatus
Teres major
Latissimus dorsi
White adipose tissue

Fig. 3. Oblique view of the right clavo-scapular brown adipose tissue deposit of *Myotis lucifugus*.

Fig. 4. Oblique view of the origins of the arteries and the terminations of the veins that supply and drain the right clavo-scapular brown fat deposit of *Myotis lucifugus*.


Occipitalis
Semispinalis capitis
Transverse cervical artery
Transverse cervical vein
Splenius capitis
Levator scapulae
Supraspinatus
Rhomboideus minor
Rhomboideus major
Infraspinatus
Teres major
Latissimus dorsi
Parotid gland
Jugular B.A.T.
Clavo-scapular B.A.T.
Spinodeltoideus
Wing

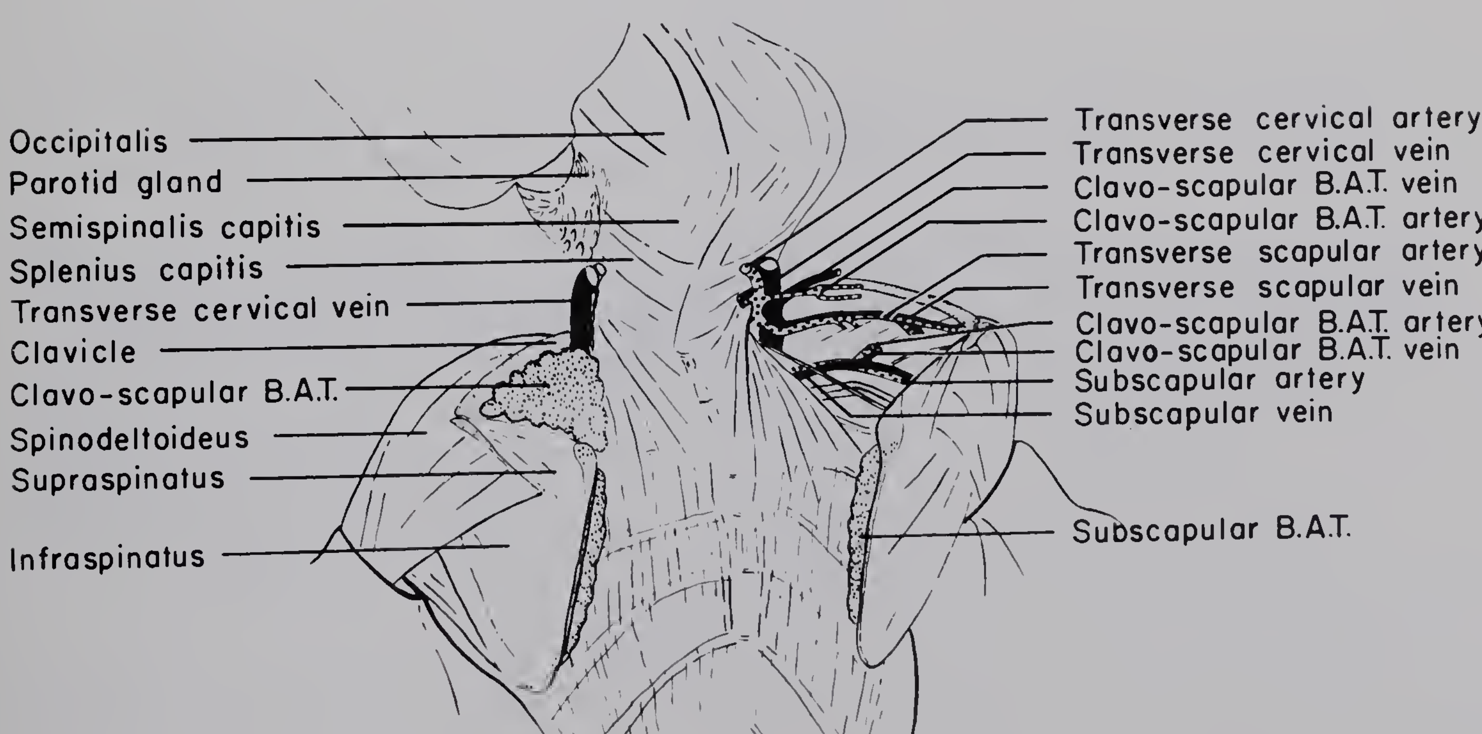
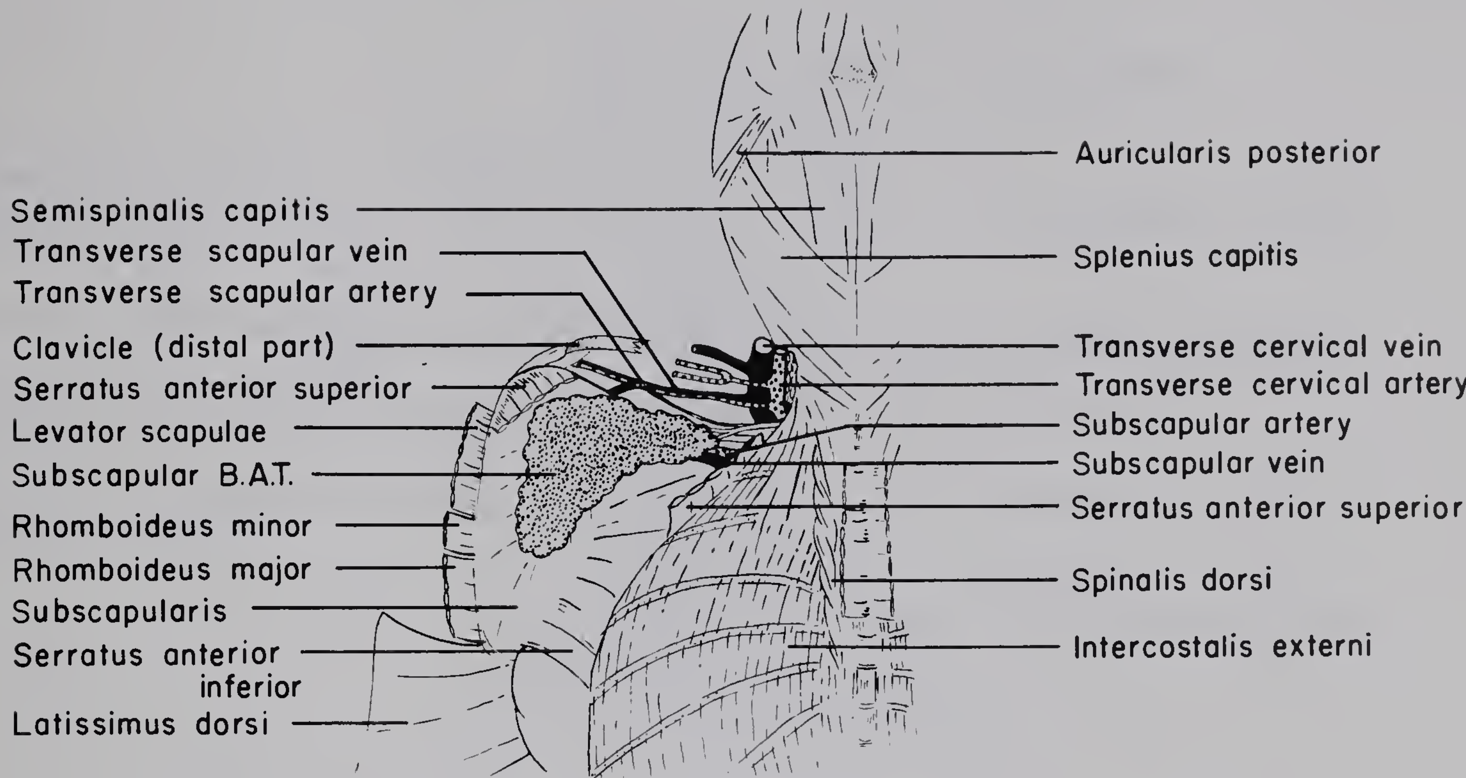

Occipitalis
Parotid gland
Semispinalis capitis
Splenius capitis
Transverse cervical vein
Clavicle
Clavo-scapular B.A.T.
Spinodeltoideus
Supraspinatus
Infraspinatus
Transverse cervical artery
Transverse cervical vein
Clavo-scapular B.A.T. vein
Clavo-scapular B.A.T. artery
Transverse scapular artery
Transverse scapular vein
Clavo-scapular B.A.T. artery
Clavo-scapular B.A.T. vein
Subscapular artery
Subscapular vein
Subscapular B.A.T.

Fig. 5. Dorsal view of the left thorax of *Myotis lucifugus*. The scapula is rotated through an angle of 180 degrees so as to reveal the subscapular brown adipose tissue.

Fig. 6. Dorsal view of the left thorax of *Myotis lucifugus*. The scapula is rotated through an angle of 180 degrees so as to reveal the subscapular B.A.T. arteries and veins.


Auricularis posterior
Semispinalis capitis
Transverse scapular vein
Transverse scapular artery
Splenius capitis
Clavicle (distal part)
Serratus anterior superior
Levator scapulae
Subscapular B.A.T.
Rhomboideus minor
Rhomboideus major
Subscapularis
Serratus anterior inferior
Latissimus dorsi
Transverse cervical vein
Transverse cervical artery
Subscapular artery
Subscapular vein
Serratus anterior superior
Spinalis dorsi
Intercostalis externi

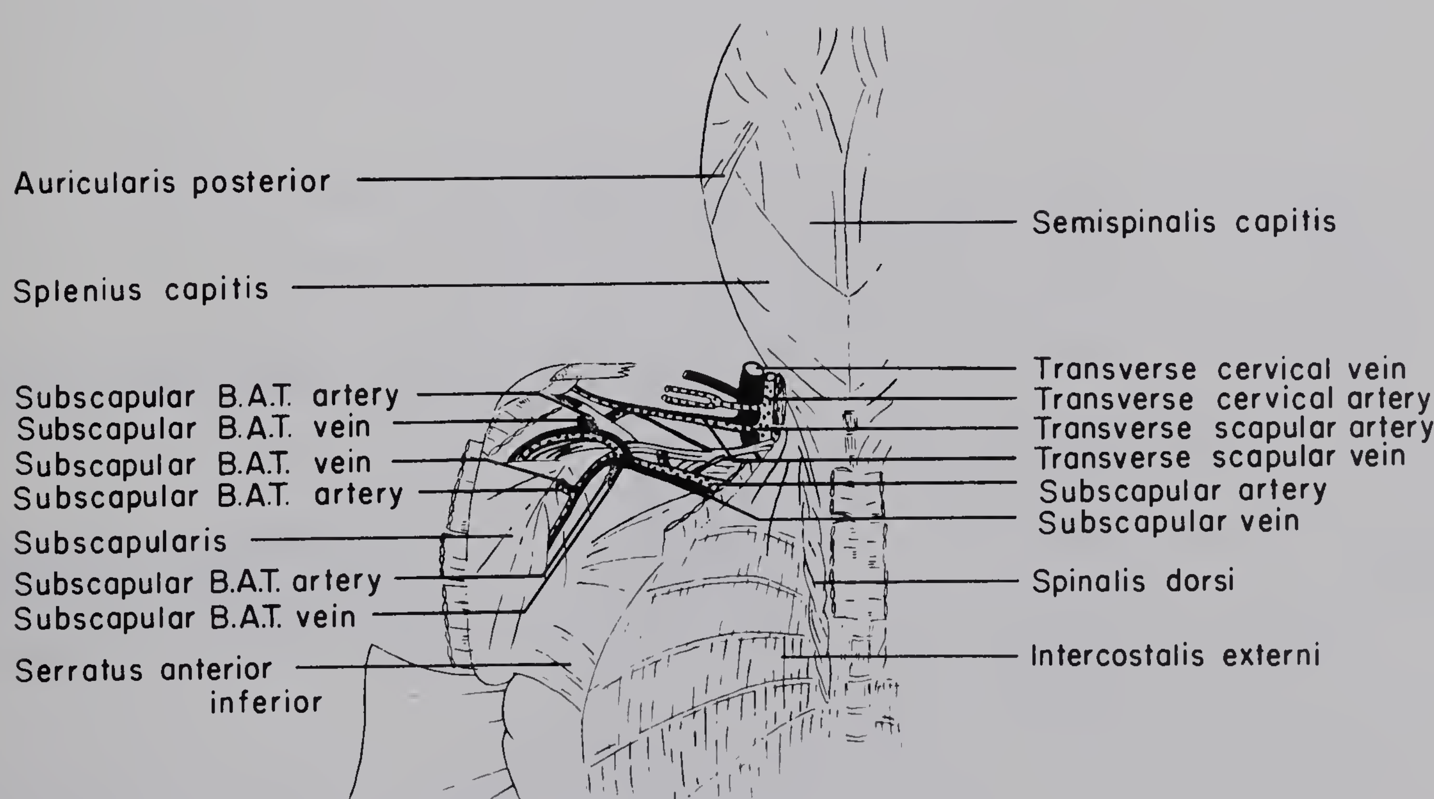
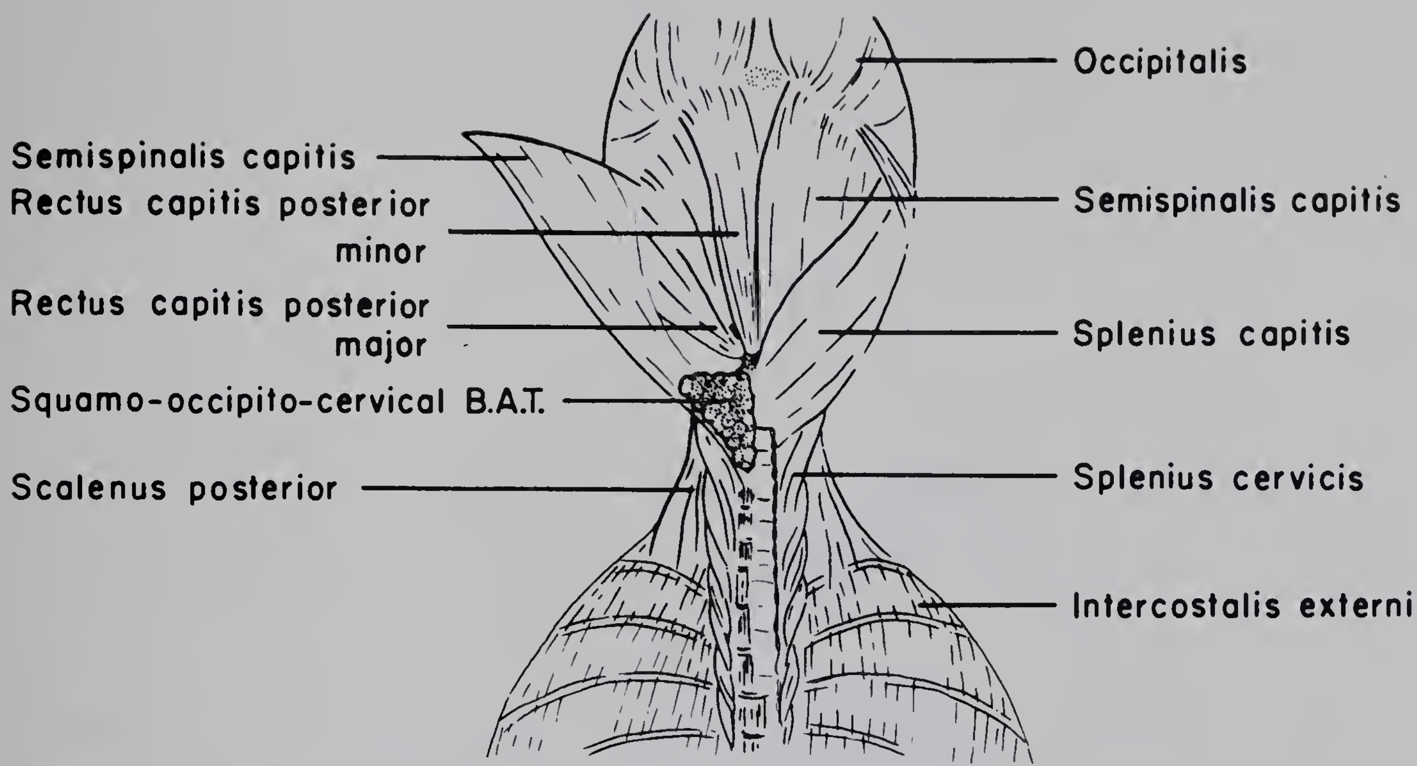

Auricularis posterior
Semispinalis capitis
Splenius capitis
Subscapular B.A.T. artery
Subscapular B.A.T. vein
Subscapular B.A.T. vein
Subscapular B.A.T. artery
Subscapularis
Subscapular B.A.T. artery
Subscapular B.A.T. vein
Serratus anterior inferior
Transverse cervical vein
Transverse cervical artery
Transverse scapular artery
Transverse scapular vein
Subscapular artery
Subscapular vein
Spinalis dorsi
Intercostalis externi

Fig. 7. Dorsal aspect of the head and neck region of *Myotis lucifugus*. The left squamo-occipito-cervical brown adipose tissue deposit is delineated.

Fig. 8. Dorsal aspect of the head and neck region of *Myotis lucifugus*. The deep cervical artery *(Profunda cervicalis)* and the posterior cervical tributary of the superior intercostal vein are delineated. Branches of these vessels supply and drain the squamo-occipito-cervical brown adipose tissue.


Occipitalis
Semispinalis capitis
Rectus capitis posterior minor
Semispinalis capitis
Rectus capitis posterior major
Splenius capitis
Squamo-occipito-cervical B.A.T.
Scalenus posterior
Splenius cervicis
Intercostalis externi

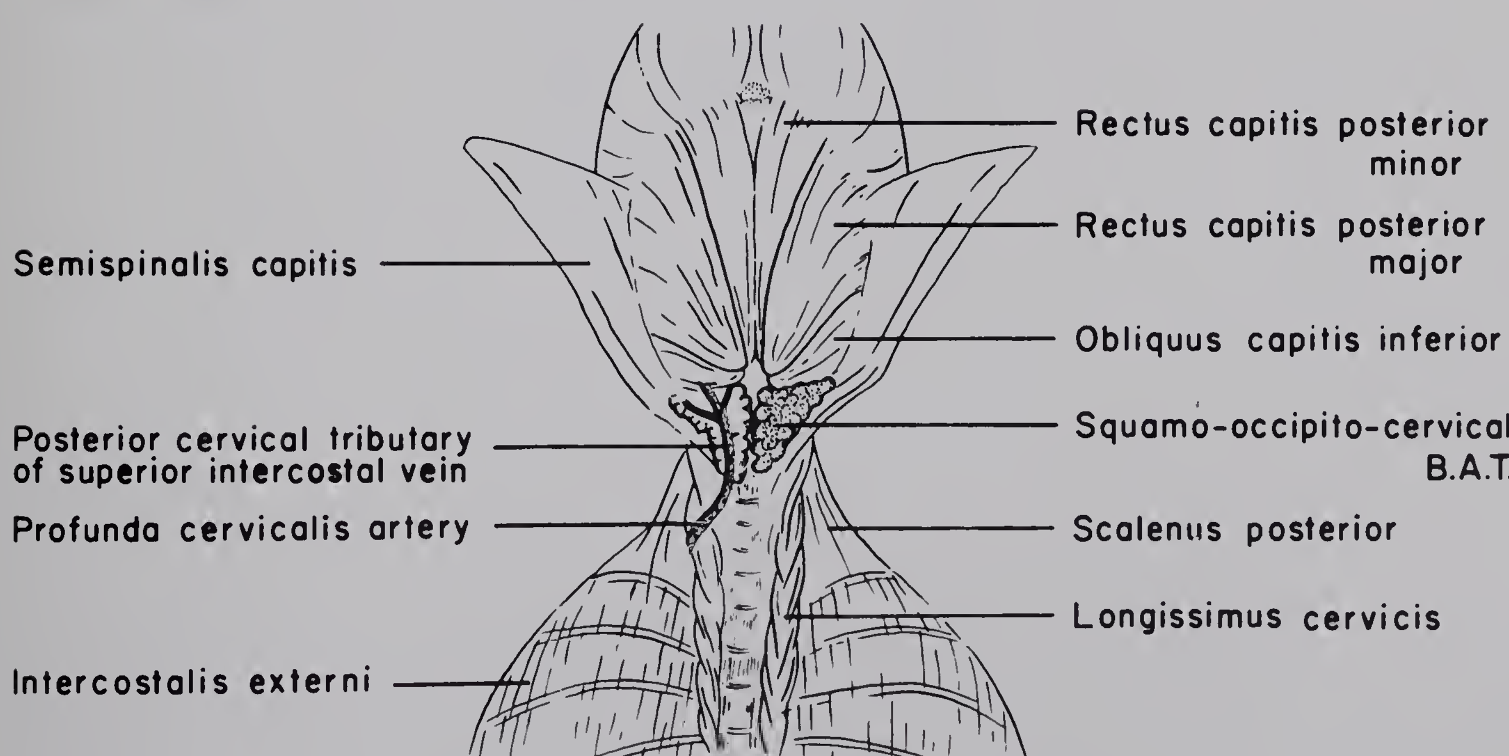

Rectus capitis posterior minor
Rectus capitis posterior major
Semispinalis capitis
Obliquus capitis inferior
Posterior cervical tributary of superior intercostal vein
Squamo-occipito-cervical B.A.T.
Profunda cervicalis artery
Scalenus posterior
Longissimus cervicis
Intercostalis externi

Fig. 9. Ventral view of the right jugular brown adipose tissue of *Myotis lucifugus*.

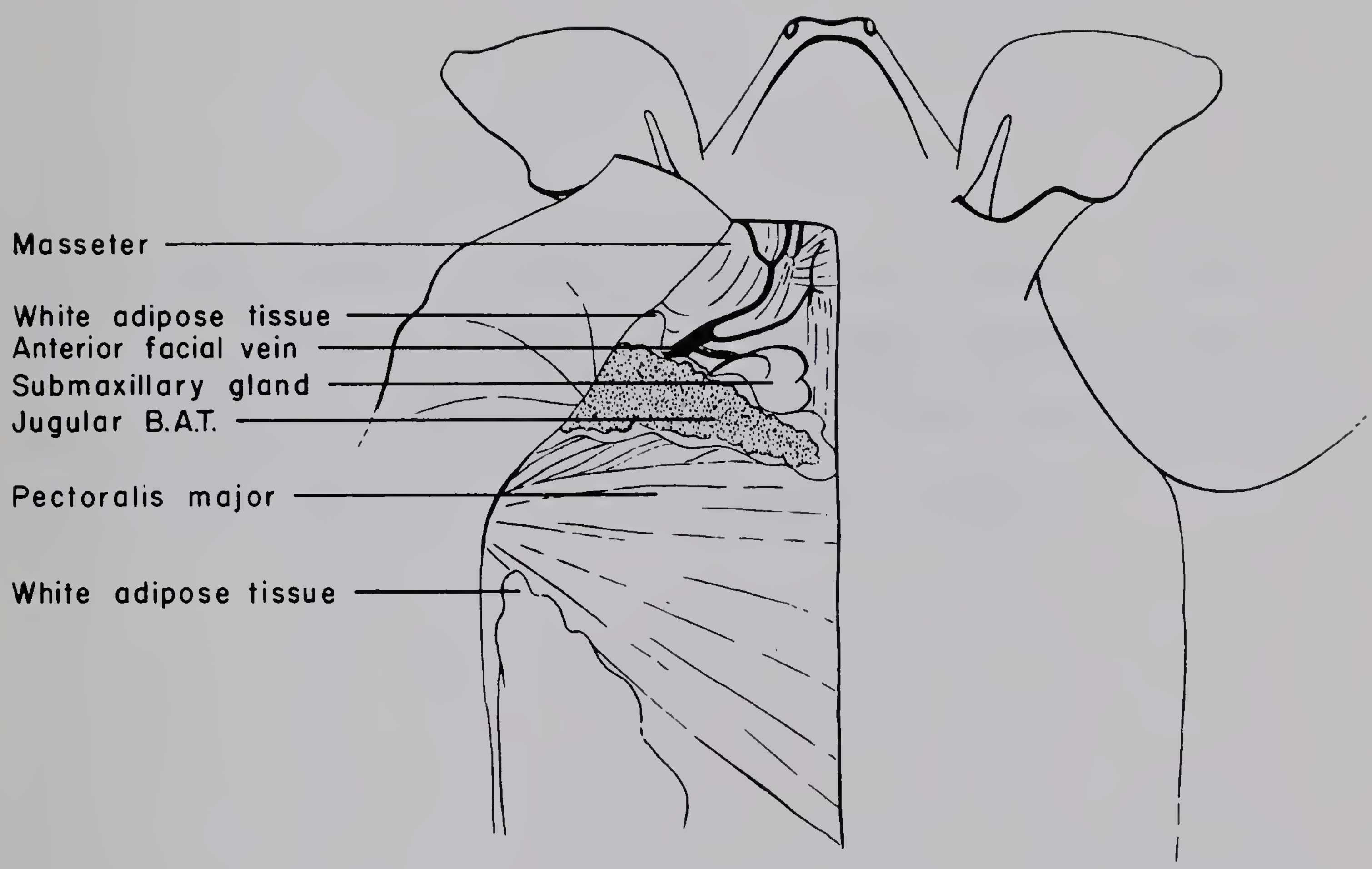
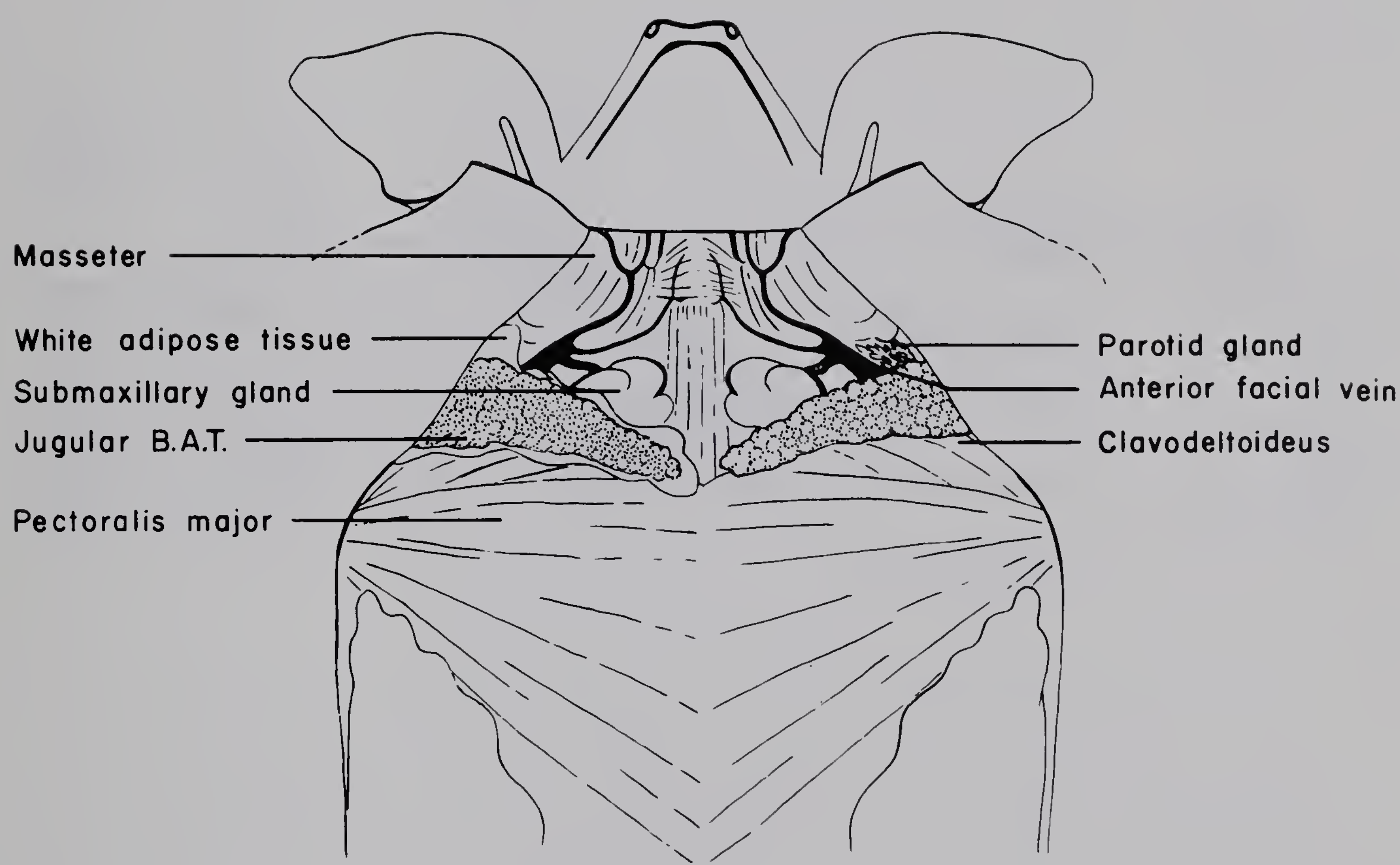

Masseter
White adipose tissue
Anterior facial vein
Submaxillary gland
Jugular B.A.T.
Pectoralis major
White adipose tissue

Fig. 10. Ventral view of the right and left jugular brown adipose tissue deposits of *Myotis lucifugus*. The white adipose tissue surrounding the jugular brown fat deposits is removed on the left side.



Masseter
White adipose tissue
Submaxillary gland
Jugular B.A.T.
Pectoralis major
Parotid gland
Anterior facial vein
Clavodeltoideus

Fig. 11. Ventral view of the left carotid brown adipose tissue deposit of *Myotis lucifugus*. The severed ends of the arteries and veins which supply and drain the left jugular brown fat deposit are demonstrated.

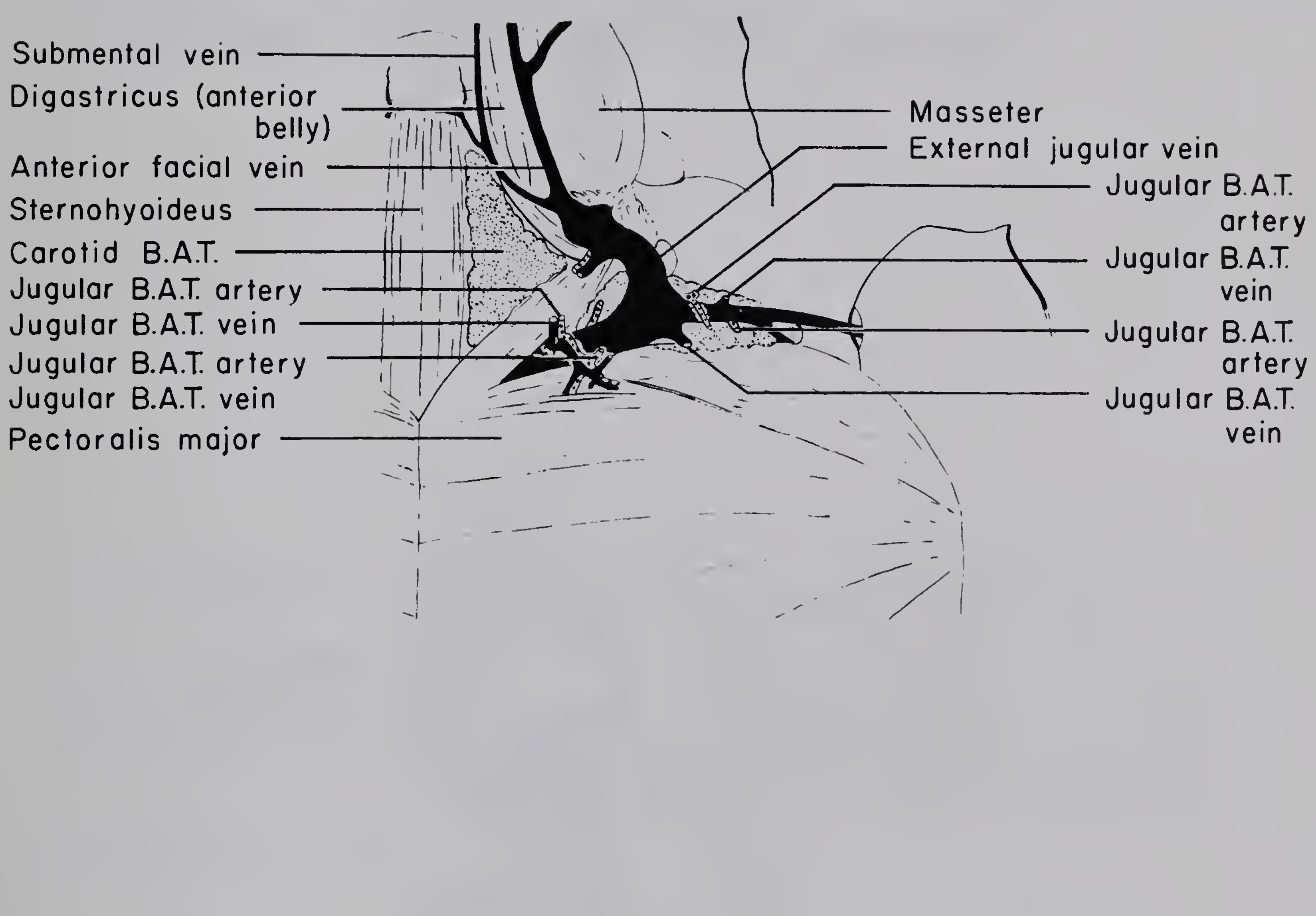
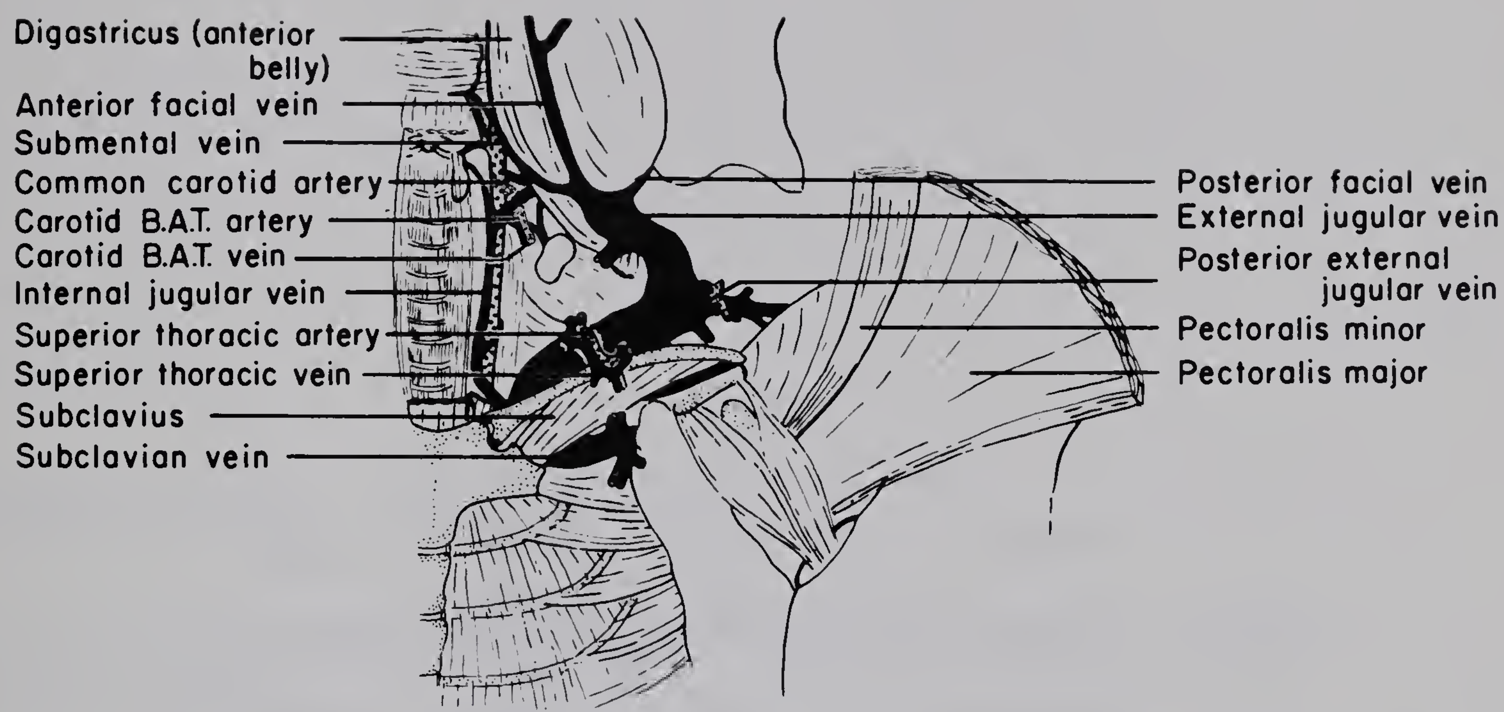
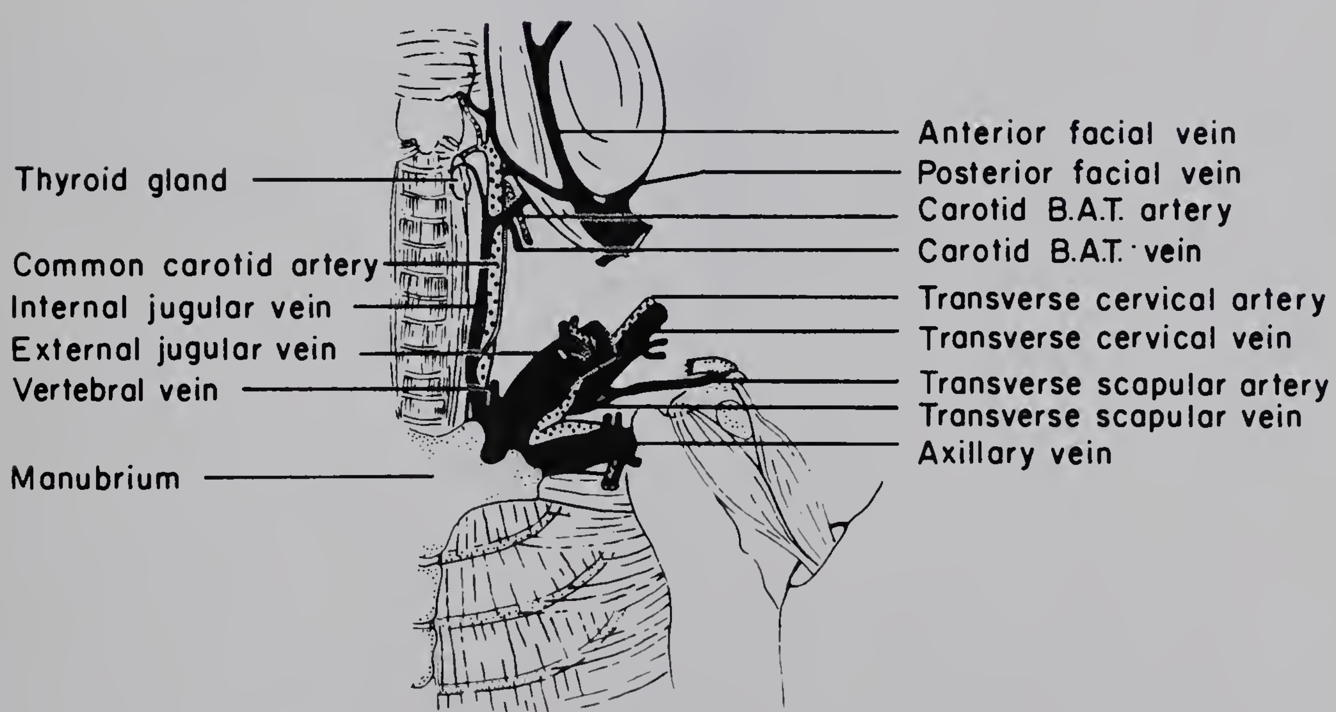

Submental vein
Digastricus (anterior belly)
Anterior facial vein
Sternohyoideus
Carotid B.A.T.
Jugular B.A.T. artery
Jugular B.A.T. vein
Jugular B.A.T. artery
Jugular B.A.T. vein
Pectoralis major
Masseter
External jugular vein
Jugular B.A.T. artery
Jugular B.A.T. vein
Jugular B.A.T. artery
Jugular B.A.T. vein

Fig. 12. Ventral view of the left neck region of *Myotis lucifugus*. The origin of the artery that supplies the left carotid brown adipose tissue deposit and the vein that drains this tissue are shown.

Fig. 13. Ventral view of the left transverse cervical vessels and the left carotid B.A.T. vessels of *Myotis lucifugus*.



Digastricus (anterior belly)
Anterior facial vein
Submental vein
Common carotid artery
Carotid B.A.T. artery
Carotid B.A.T. vein
Internal jugular vein
Superior thoracic artery
Superior thoracic vein
Subclavius
Subclavian vein
Posterior facial vein
External jugular vein
Posterior external jugular vein
Pectoralis minor
Pectoralis major



Thyroid gland
Common carotid artery
Internal jugular vein
External jugular vein
Vertebral vein
Manubrium
Anterior facial vein
Posterior facial vein
Carotid B.A.T. artery
Carotid B.A.T. vein
Transverse cervical artery
Transverse cervical vein
Transverse scapular artery
Transverse scapular vein
Axillary vein

Fig. 14. Ventral view of the origins of the arteries which supply the left jugular and carotid brown adipose tissue deposits in *Myotis lucifugus*.

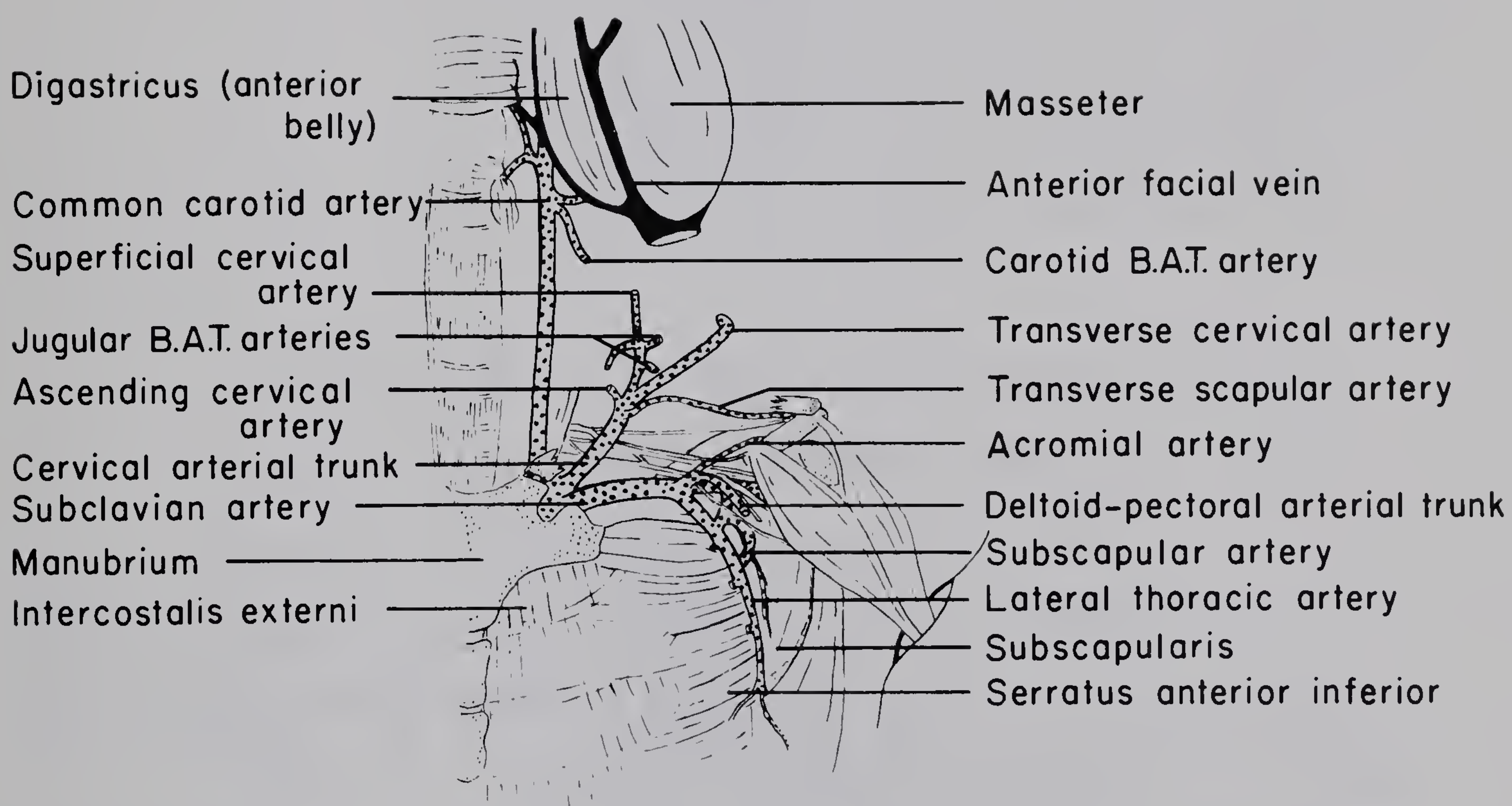
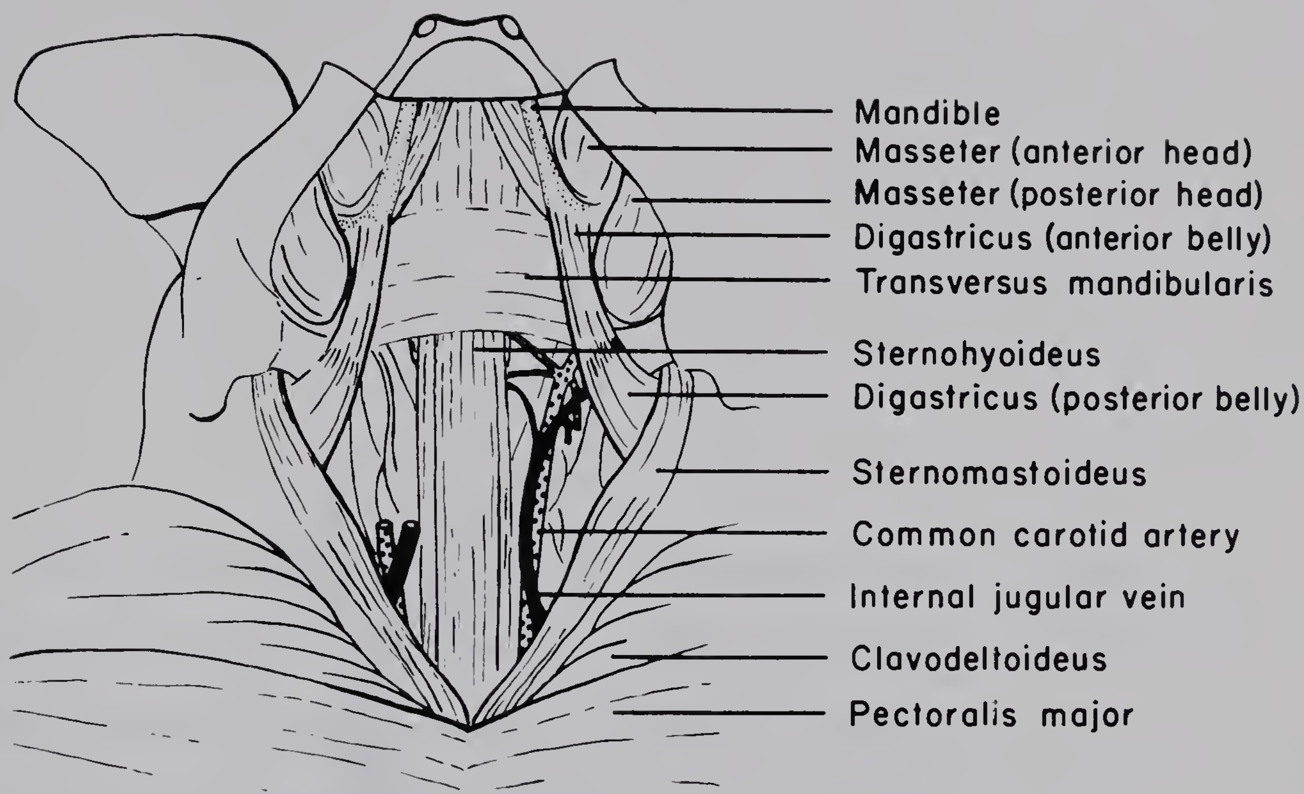
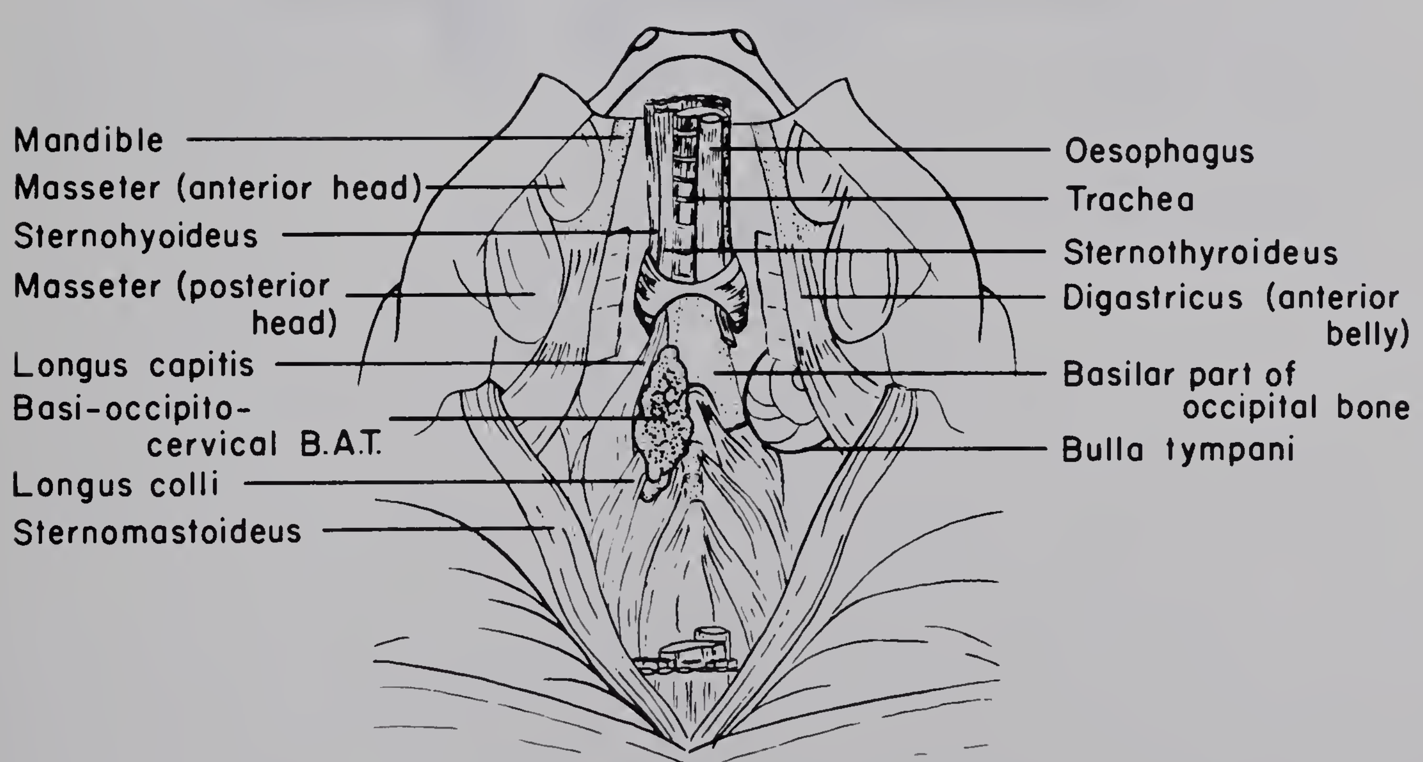

Digastricus (anterior belly)
Common carotid artery
Superficial cervical artery
Jugular B.A.T. arteries
Ascending cervical artery
Cervical arterial trunk
Subclavian artery
Manubrium
Intercostalis externi
Masseter
Anterior facial vein
Carotid B.A.T. artery
Transverse cervical artery
Transverse scapular artery
Acromial artery
Deltoid-pectoral arterial trunk
Subscapular artery
Lateral thoracic artery
Subscapularis
Serratus anterior inferior

Fig. 15. Ventral view of the head and neck of *Myotis lucifugus*. The carotid brown adipose tissue deposit is removed to show the common carotid arteries and internal jugular veins.

Fig. 16. An illustration of the base of the skull and the deep aspect of the ventral neck region of *Myotis lucifugus*. The right lobe of the basi-occipito-cervical brown fat deposit is shown; the left lobe is removed to reveal the underlying structures of this tissue.



Mandible
Masseter (anterior head)
Masseter (posterior head)
Digastricus (anterior belly)
Transversus mandibularis
Sternohyoideus
Digastricus (posterior belly)
Sternomastoideus
Common carotid artery
Internal jugular vein
Clavodeltoideus
Pectoralis major



Mandible
Masseter (anterior head)
Sternohyoideus
Masseter (posterior head)
Longus capitis
Basi-occipito-cervical B.A.T.
Longus colli
Sternomastoideus
Oesophagus
Trachea
Sternothyroideus
Digastricus (anterior belly)
Basilar part of occipital bone
Bulla tympani

Fig. 17. An illustration of the base of the skull and the deep aspect of the ventral neck region of *Myotis lucifugus*. The terminal portions of the veins from the basi-occipito-cervical brown fat deposit are shown. The artery to the left basi-occipito-cervical B.A.T. is delineated.

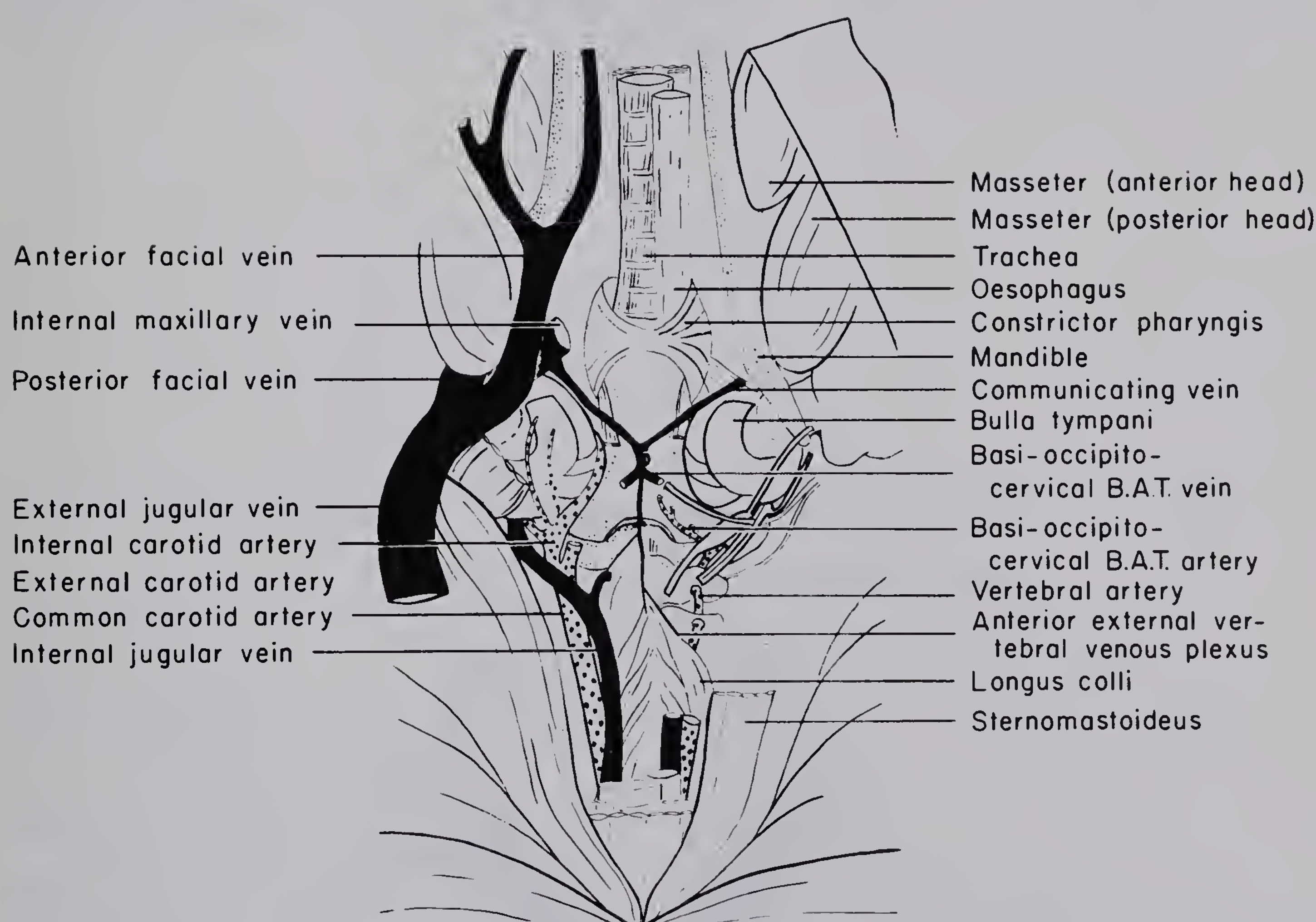
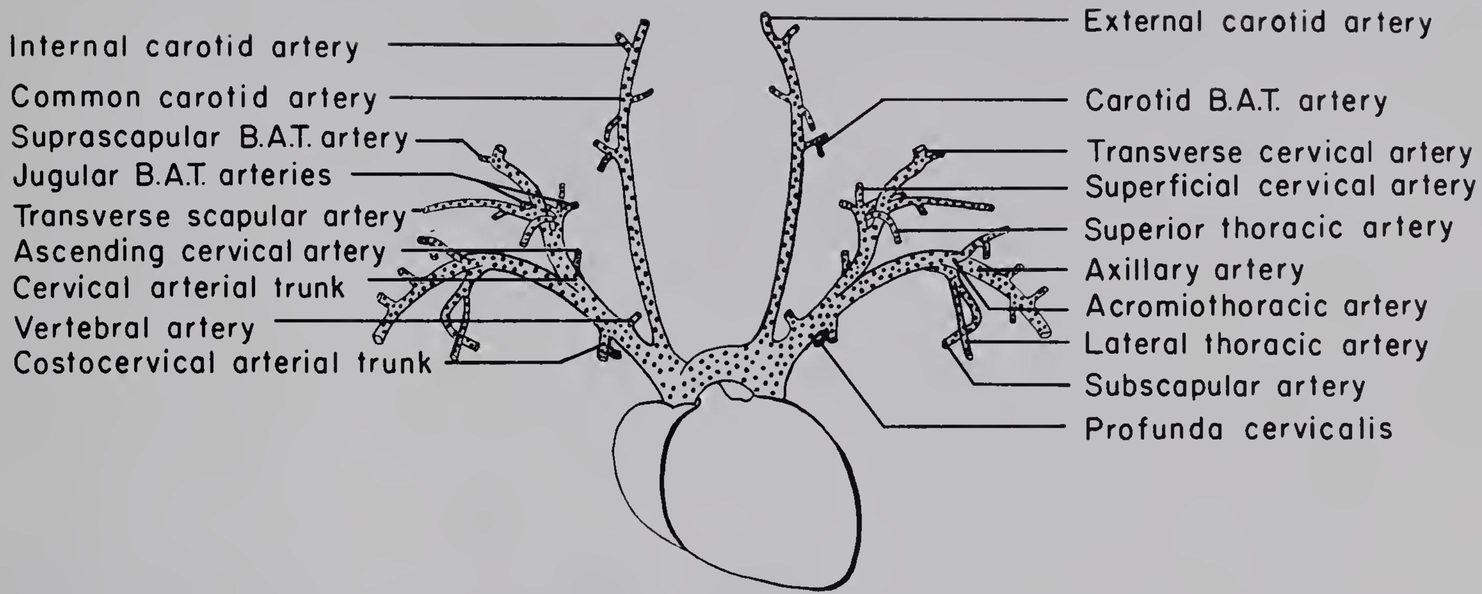

Anterior facial vein
Internal maxillary vein
Posterior facial vein
External jugular vein
Internal carotid artery
External carotid artery
Common carotid artery
Internal jugular vein
Masseter (anterior head)
Masseter (posterior head)
Trachea
Oesophagus
Constrictor pharyngis
Mandible
Communicating vein
Bulla tympani
Basi-occipito-cervical B.A.T. vein
Basi-occipito-cervical B.A.T. artery
Vertebral artery
Anterior external vertebral venous plexus
Longus colli
Sternomastoideus

Fig. 18. Diagram of the origin of the major anterior arteries of *Myotis lucifugus*.

Fig. 19. Diagram of the terminations of the major anterior veins of *Myotis lucifugus*.


Internal carotid artery
Common carotid artery
Suprascapular B.A.T. artery
Jugular B.A.T. arteries
Transverse scapular artery
Ascending cervical artery
Cervical arterial trunk
Vertebral artery
Costocervical arterial trunk
External carotid artery
Carotid B.A.T. artery
Transverse cervical artery
Superficial cervical artery
Superior thoracic artery
Axillary artery
Acromiothoracic artery
Lateral thoracic artery
Subscapular artery
Profunda cervicalis

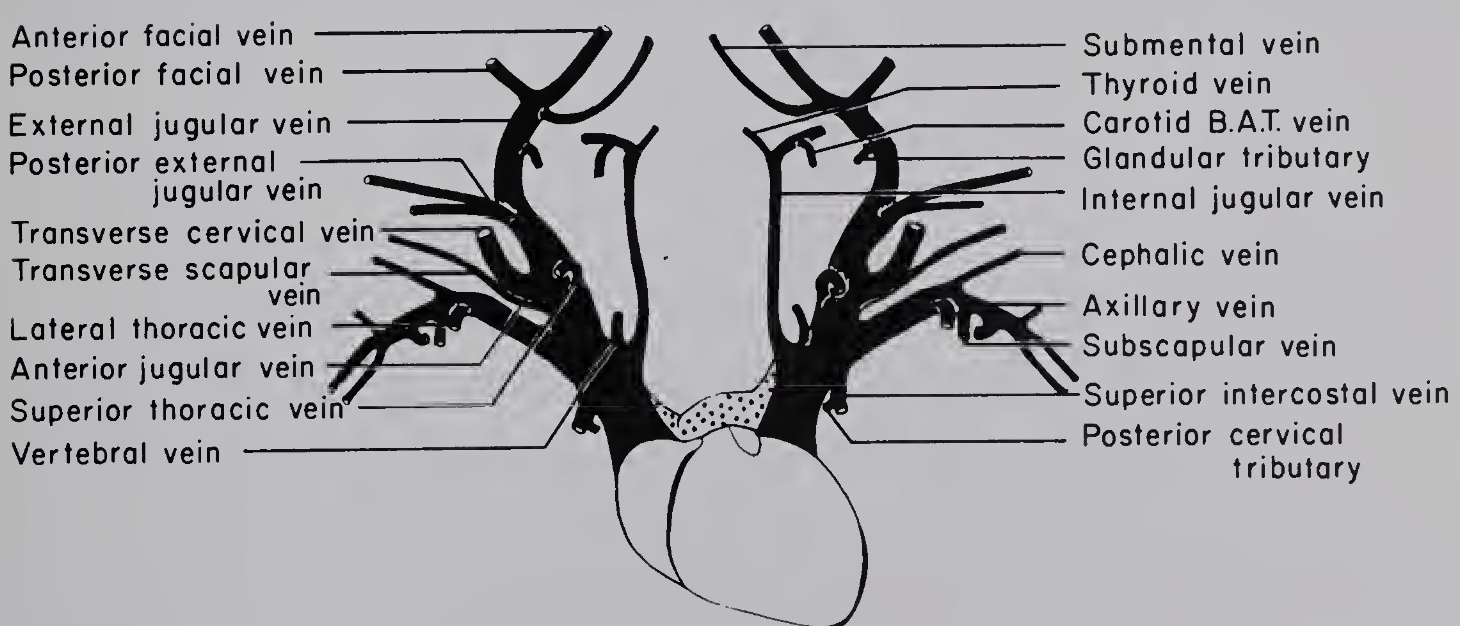
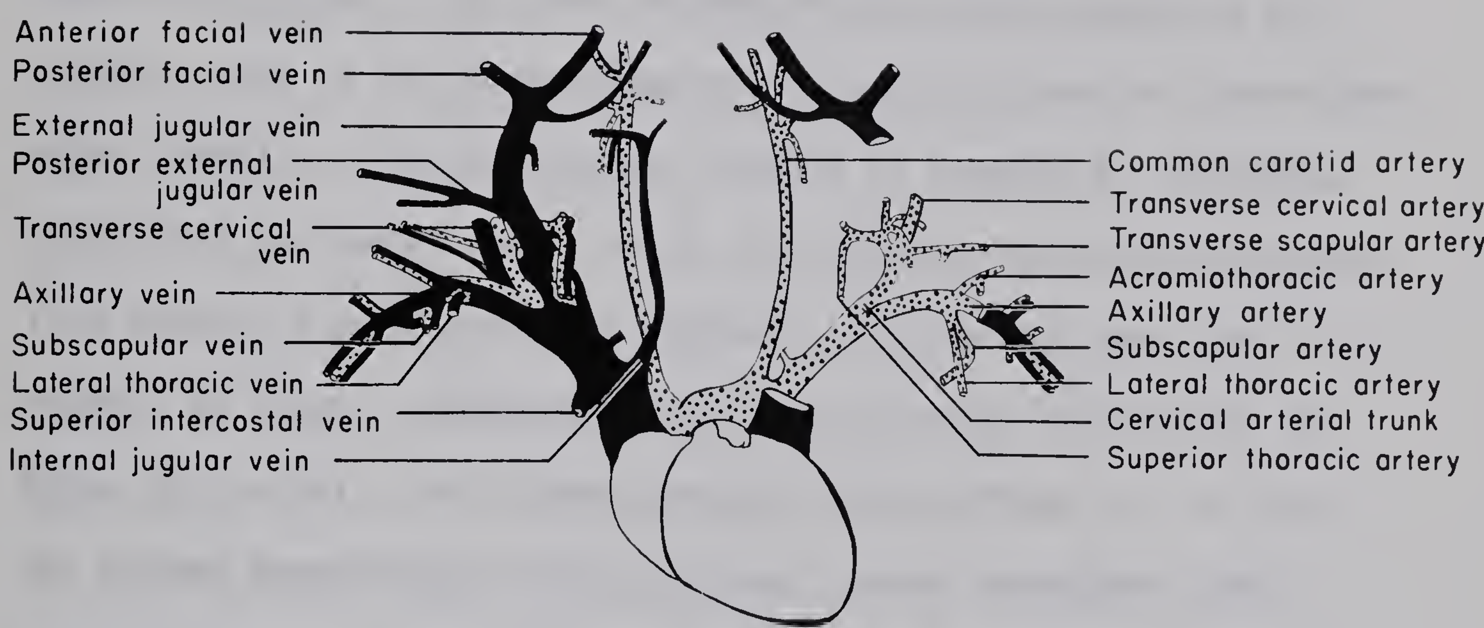

Anterior facial vein
Posterior facial vein
External jugular vein
Posterior external jugular vein
Transverse cervical vein
Transverse scapular vein
Lateral thoracic vein
Anterior jugular vein
Superior thoracic vein
Vertebral vein
Submental vein
Thyroid vein
Carotid B.A.T. vein
Glandular tributary
Internal jugular vein
Cephalic vein
Axillary vein
Subscapular vein
Superior intercostal vein
Posterior cervical tributary

Fig. 20. Diagram of the relationship between the major anterior arteries and veins of *Myotis lucifugus*.



Anterior facial vein
Posterior facial vein
External jugular vein
Posterior external jugular vein
Transverse cervical vein
Axillary vein
Subscapular vein
Lateral thoracic vein
Superior intercostal vein
Internal jugular vein
Common carotid artery
Transverse cervical artery
Transverse scapular artery
Acromiothoracic artery
Axillary artery
Subscapular artery
Lateral thoracic artery
Cervical arterial trunk
Superior thoracic artery

Deer mice

1. External Thoracic Brown Adipose Tissue

a) Interscapular B.A.T.

The interscapular brown fat deposit (Figs. 21, 22) occupies the scapular depression in the dorsal thoracic region. It is a bilobed structure which extends from approximately the first to the twelfth thoracic vertebra. The medial surfaces of the two lobes are in close contact with each other in the mid-dorsal line of the animal. They are separated, however, by connective tissue. The deep surface of the interscapular B.A.T. overlies part of the *Acromiotrapezius* cranially, and the *Rhomboideus major* caudally. Its superficial surface is covered by integument except for the caudal part, which is covered by the *Spinotrapezius*. This muscle is seen partially embedded in brown fat when the deposit is large. Furthermore, with an increase in the mass of brown fat in fall, the thoraco-dorsal vessels (Figs. 21, 22, 23, 25) become surrounded by brown adipose tissue throughout their entire course.

Arterial supply. In the deer mouse, as in the rat (Greene, 1959; Smith and Roberts, 1964), the interscapular B.A.T. is supplied by the thoracodorsal artery (Figs. 21, 22, 23, 25, 41). This finding contrasts with that in the bat, where the interscapular brown fat deposit is supplied by the transverse cervical artery.

The thoracodorsal artery is a continuation of the sub-scapular artery (Figs. 41, 48, 50). It runs in a ventro-dorsal direction, closely following the axillary border of the scapula. On the dorsal side of the animal, the artery emerges between the

Teres major and *Latissimus dorsi*. After a brief superficial course, it enters the interscapular brown fat deposit. Within this deposit the thoracodorsal artery divides into two or three terminal branches (Fig. 25). In the rat (Smith and Roberts, 1964), this artery extends beyond the interscapular B.A.T. to supply a second brown fat deposit in the dorsal cervical region.

The thoracodorsal artery supplies adjacent muscles throughout its course. It gives branches to the *Subscapularis*, *Teres major*, *Latissimus dorsi*, *Serratus anterior*, *Cutaneus maximus*, and *Spinotrapezius*.

Venous drainage. The interscapular brown fat deposit is drained by a complicated venous shunt system (Figs. 25, 26). Multitudinous venules give rise to three or four veins within the brown fat deposit. The right and left thoracodorsal veins unite to form "Sulzer's vein" (Figs. 13, 25, 26) near the mid-dorsal line of the animal. Named after its discoverer, Sulzer's vein was described first in the European hamster (Sulzer, 1774). Its presence has been demonstrated also in the rat by Smith and Roberts (1964).

In the deer mouse, Sulzer's vein receives two tributaries (Fig. 25). A superior tributary, formed by the union of several venules from the *Trapezius*, arises in the cranial neck region. It courses caudally along the mid-dorsal line of the animal, under cover of the interscapular brown fat deposit. The vein receives a number of small vessels from adjacent muscles and makes several cross-connections with the posterior external vertebral plexus. The inferior tributary arises in the mid-lumbar region and is

essentially a mirror image of the superior tributary. It communicates also with the vertebral vein system.

Sulzer's vein penetrates the intercostal muscles between the fourth and the fifth rib, to the left of the vertebral column. Upon entering the thoracic cavity, this short vessel empties into the azygos vein. In *P. maniculatus*, the azygos vein lies to the left of the vertebral column. It crosses in front of the dorsal aorta at the level of the fourth rib to join the "left" superior vena cava. This vein descends behind the heart and in conjunction with the inferior vena cava, empties into the right atrium.

At this point, a brief explanation of the diversity in the intrathoracic vein system in mammals is necessary. In man and domestic animals (Krahmer, 1964), the left innominate vein crosses in front of the aortic arch to join its right counterpart in the formation of a superior vena cava. The azygos vein, which lies to the right of the vertebral column, empties into the single superior vena cava. In the elephant (Krahmer, 1964) and a variety of small mammals (Halpern, 1953; Greene, 1959; Schwarze, Michel, and Apitsch, 1961; Krahmer, 1964), including the deer mouse and little brown bat (present investigation), the innominate veins do not unite. They course toward the heart as independent superior or cranial venae cavae. A "vena azygos sinistra" is always associated with this paired superior vena caval system.

The venous route from the interscapular brown fat to the heart, via the azygos vein, comprises part of the shunt system. The other part forms a link between the veins of the interscapular B.A.T. and the axillary vein. As the thoracodorsal vein emerges

from the lateral border of the interscapular brown fat deposit, it divides into two vessels (Fig. 25). These lie parallel to each other as they course toward the axillary border of the scapula. Here, they unite again. Short veins provide cross-connections at regular intervals between the two parallel veins. The thoracodorsal artery, which lies between the thoracodorsal veins, is in direct contact with this venous plexus. The single thoracodorsal vein continues along the axillary border to become the subscapular vein in the axillary region. The latter vessel joins the axillary vein, which, in turn, becomes the subclavian vein, innominate vein, and finally the superior vena cava. Thus, the venous system through the interscapular brown fat deposit forms a complete circuit, or shunt.

The thoracodorsal vein receives a number of tributaries which correspond closely to the branches of the thoracodorsal artery.

b) Subscapular B.A.T.

The subscapular B.A.T. (Figs. 27, 30, 31) is situated between the scapula and the thoracic cage. It overlies some external intercostal muscles ventrally, and it is covered dorsally by the *Serratus anterior*. This muscle, because of its extensive insertion along the vertebral border of the scapula, lies between the *Subscapularis* and the subscapular B.A.T. In this respect, the location of the subscapular brown fat deposit in the deer mouse deviates slightly from that in the bat. The deep branch of the thyrocervical arterial trunk and corresponding vein are surrounded by this adipose tissue. When large, the subscapular B.A.T.

extends forward over the anterior border of the *Serratus anterior*, where it merges with the axillary B.A.T. (Fig. 38).

Arterial supply. The subscapular B.A.T. is supplied by a number of small arteries which arise from the deep branch of the thyrocervical arterial trunk (Figs. 30, 31, 41, 48, 50).

The deep branch of the thyrocervical arterial trunk corresponds to the deep branch of the ascending cervical artery in the rat (Greene, 1959). It is the vessel which supplies the deep muscles of the neck and upper back.

Venous drainage. The subscapular B.A.T. is drained by a number of small vessels which terminate in the deep tributary of the anterior jugular vein (Figs. 30, 31, 42, 49, 50).

c) Axillary B.A.T.

The axillary brown fat deposit (Figs. 38, 39, 40) is situated in the axilla, where it fills the entire space of the fossa. It surrounds the axillary vessels, the brachial plexus, and one or two lymph nodes. The deposit is continuous with the subscapular B.A.T. when the mass of brown fat is large.

Arterial supply. The axillary B.A.T. is supplied by a relatively large branch (Fig. 40) of the subscapular artery (Figs. 40, 41, 48, 50). In large deposits, additional branches from the subclavian artery and humeral circumflex are present.

Venous drainage. The axillary B.A.T. is drained by a tributary (Fig. 42) of the subscapular vein (Figs. 42, 43, 49, 50). In addition, tributaries of the axillary and/or subclavian vein are present when the deposit is large.

2. Neck Region Brown Adipose Tissue

a) Transverse cervical B.A.T.

This deposit (Figs. 27, 28, 30) occupies the space between the skull and the superior aspect of the scapula. Each of the lobes extends from the vertebral column to the side of the neck. They are separated from each other medially by the muscles of the shoulder girdle, which originate from the spinous processes of the cervical vertebrae. The transverse cervical brown fat overlies the *Splenius capitis;* it is covered by the *Occipito-scapularis* and *Acromiotrapezius*. When large, this deposit merges with the subscapular B.A.T. (Figs. 27, 30, 31) caudally, and the jugular B.A.T. (Figs. 34, 35, 37) ventrally.

A comparison between the two species shows that the disposition of the extensive interscapular B.A.T. in the bat is such as to correspond to a combination of the transverse cervical and interscapular brown fat deposits in the deer mouse (Figs. 1, 21, 27). The discontinuity between these two deposits in the deer mouse is likely related to the morphology of the muscles of the shoulder girdle. They are important in the movement of the scapula and shoulder during walking but probably not in flight. In the bat, where these muscles are small, the scapular depression is continuous with the space between the scapula and the head (Fig. 2). The hollow in the neck region is particularly deep because of the marked cervical lordosis in this animal. A voluminous space is available for the expansion of the interscapular brown adipose tissue. In the deer mouse, the gap in the neck region is separated from the scapular depression by the extensive *Trapezius* (Fig. 23).

One might interpret these facts to mean that the presence of a transverse cervical deposit in the deer mouse is an alternative development for maximizing the amount of brown adipose tissue in the external thoracic and neck regions.

Arterial supply. The transverse cervical B.A.T. is supplied by numerous small vessels from the transverse cervical artery (Figs. 24, 29, 36, 41, 48, 50).

Venous drainage. The transverse cervical B.A.T. is drained by small tributaries of the transverse cervical vein (Figs. 24, 29, 42, 49, 50).

The functional diversity of the transverse cervical vessels needs to be emphasized. In the deer mouse, these vessels supply and drain numerous muscles, most of which are associated with the movement of the shoulder girdle in walking. In the bat, where the forelimbs are not used for walking, and where the interscapular brown adipose tissue is the largest deposit and the most important source of heat production during arousal from hibernation (Hayward and Lyman, 1967), the vessels serve primarily the requirements of this deposit but not nearby muscles.

b) Squamo-occipito-cervical B.A.T.

The squamo-occipito-cervical B.A.T. (Figs. 31, 32) is situated in the deep dorsal neck region. It is covered by the *Semispinalis capitis* dorsally, and overlies the *Semispinalis cervicis*, *Rectus capitis*, and *Obliquus capitis* ventrally. The two portions of the bilobed structure extend from the occiput of the skull to the upper thorax. They meet in the mid-dorsal line but are separated from each other by connective tissue. The strip-like lobes expand in a lateral direction in the head region only.

These expansions surround the occipital artery, posterior auricular vein, and the cervical plexus of spinal nerves. The deep cervical artery *(Profunda cervicalis)* and corresponding vein are embedded in the elongated portion of the brown fat deposit.

Arterial supply. The squamo-occipito-cervical B.A.T. is supplied by numerous arterioles from the *Profunda cervicalis* (Figs. 32, 33, 48, 50). When large, the anterior part of the brown fat deposit is supplied also by a branch of the occipital artery (Fig. 32).

Venous drainage. The squamo-occipito-cervical B.A.T. is drained by a number of venules which terminate at the posterior cervical tributary of the superior intercostal vein (Figs. 32, 33, 49, 50). Whenever the anterior part of the deposit is supplied by branches of the occipital artery, the same region is drained by venules which terminate at the posterior auricular vein (Fig. 32).

c) Jugular B.A.T.

The jugular B.A.T. (Figs. 34, 35, 37) lies dorsal to the glands in the ventral neck region. It surrounds the entire external jugular vein when the deposit is large in late autumn. When a minimum amount of brown fat exists in early summer, only the lateral surface of the vessel is covered. The jugular B.A.T. extends from the mid-ventral line to the side of the neck. An anterior extension stretches forward as far as the hyoid bone.

Arterial supply. The medial third of the jugular B.A.T. is supplied by a branch (Figs. 36, 37, 38) of the thyrocervical arterial trunk (Figs. 41, 48, 50). This artery was present in all specimens examined. Two or three arteries, which supply the

lateral portion of the jugular brown fat, arise from the ascending cervical artery (Figs. 41, 42, 48, 50).

Venous drainage. The jugular brown fat deposit is drained usually by four veins (Fig. 37) which empty, respectively, into the external jugular vein (Figs. 36, 37, 38, 50), posterior external jugular vein (Figs. 35, 37, 38, 50), anterior facial vein (Figs. 37, 50), and the parotid vein (Figs. 37, 38).

d) Carotid B.A.T.

The carotid B.A.T. lies in the carotid fossa, the depression in the ventral neck region, which is formed by the anterior belly of *Omohyoideus* in front, the *Sternomastoideus* behind, and the posterior belly of the *Digastricus* above. Within this area, the common carotid artery, internal jugular vein, thyroid vessels, hypoglossal nerve, vagus nerve, a lymph node, and occasionally, the thyroid gland are embedded in brown fat.

Arterial supply. The carotid brown fat deposit is supplied by a branch of the common carotid artery.

Venous drainage. The carotid B.A.T. is drained by a tributary of the internal jugular vein.

3. Internal Thoracic Brown Adipose Tissue

Within the thoracic cavity, the pericardial portion of the intrathoracic B.A.T. (Figs. 43, 44) occupies the space of the anterior mediastinum. It surrounds the mammary vessels ventrally, and dorsally, contacts the heart. The tissue extends backward between the innominate veins and then expands on the dorsal side of the heart. It continues along the inferior vena cava, and descending aorta. More dorsally, brown fat occupies the intercostal spaces

and covers the azygos vein. When the mass of brown fat is large, the intercostal B.A.T. from both sides of the vertebral spine expands ventrally to become continuous with the aortic B.A.T. The vagus, phrenic, and splanchnic nerves, as well as the sympathetic trunk, are in direct contact with the intrathoracic brown fat.

Arterial supply. The internal thoracic brown adipose tissue receives branches from the pericardial and/or internal mammary artery in the mediastinal region. It is supplied by branches of the phrenic artery along the inferior vena cava. The intercostal and aortic B.A.T. obtain a number of arterioles from the dorsal aorta.

Venous drainage. The venules draining the intrathoracic brown adipose tissue correspond closely to the arterioles supplying the tissue. They are tributaries of the pericardial and/or internal mammary vein, inferior vena cava, and azygos vein.

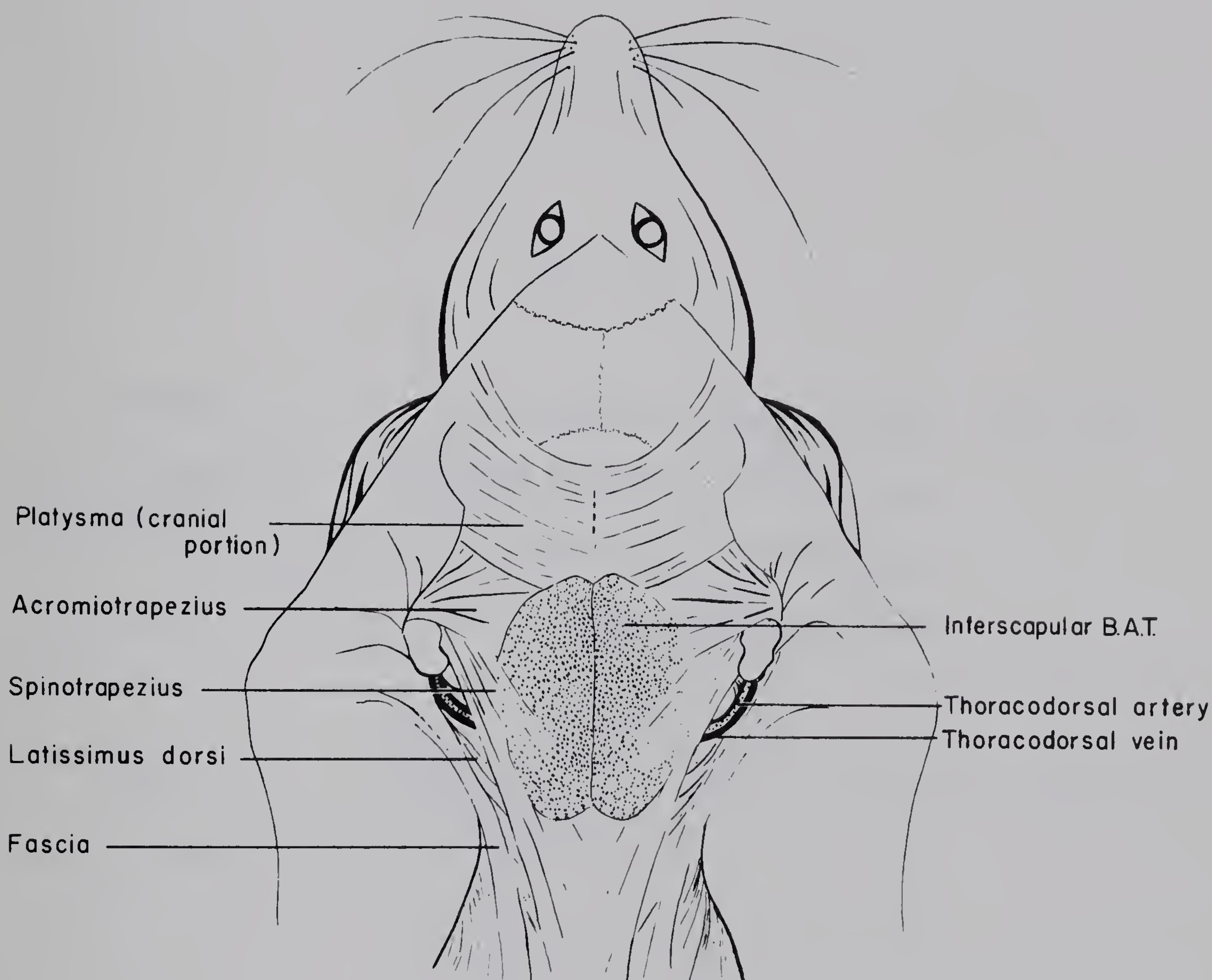
4. Abdominal Brown Adipose Tissue

The abdominal brown adipose tissue (Fig. 46) extends from the diaphragm to the level immediately caudal to the renal vessels. In this region, it encloses the inferior vena cava and abdominal aorta. The brown fat expands between the hila of the kidneys, where it surrounds the renal and suprarenal vessels. The tissue stretches also over the cranial pole of the kidney and it encloses the suprarenal gland. The abdominal and intrathoracic brown adipose tissue merge in the aortic and vena caval openings of the diaphragm.

Arterial supply. The abdominal B.A.T. is supplied by branches of the descending aorta, renal and suprarenal arteries.

Venous drainage. The abdominal B.A.T. is drained by tributaries of the inferior vena cava, renal and suprarenal vessels.

Fig. 21. Dorsal view of the interscapular brown adipose tissue (B.A.T.) of *Peromyscus maniculatus*.



Platysma (cranial portion)
Acromiotrapezius
Spinotrapezius
Latissimus dorsi
Fascia
Interscapular B.A.T.
Thoracodorsal artery
Thoracodorsal vein

Fig. 22. Dorsal view of the right lobe of the interscapular brown adipose tissue of *Peromyscus maniculatus*. The thoracodorsal vessels, which supply and drain this tissue, are shown.

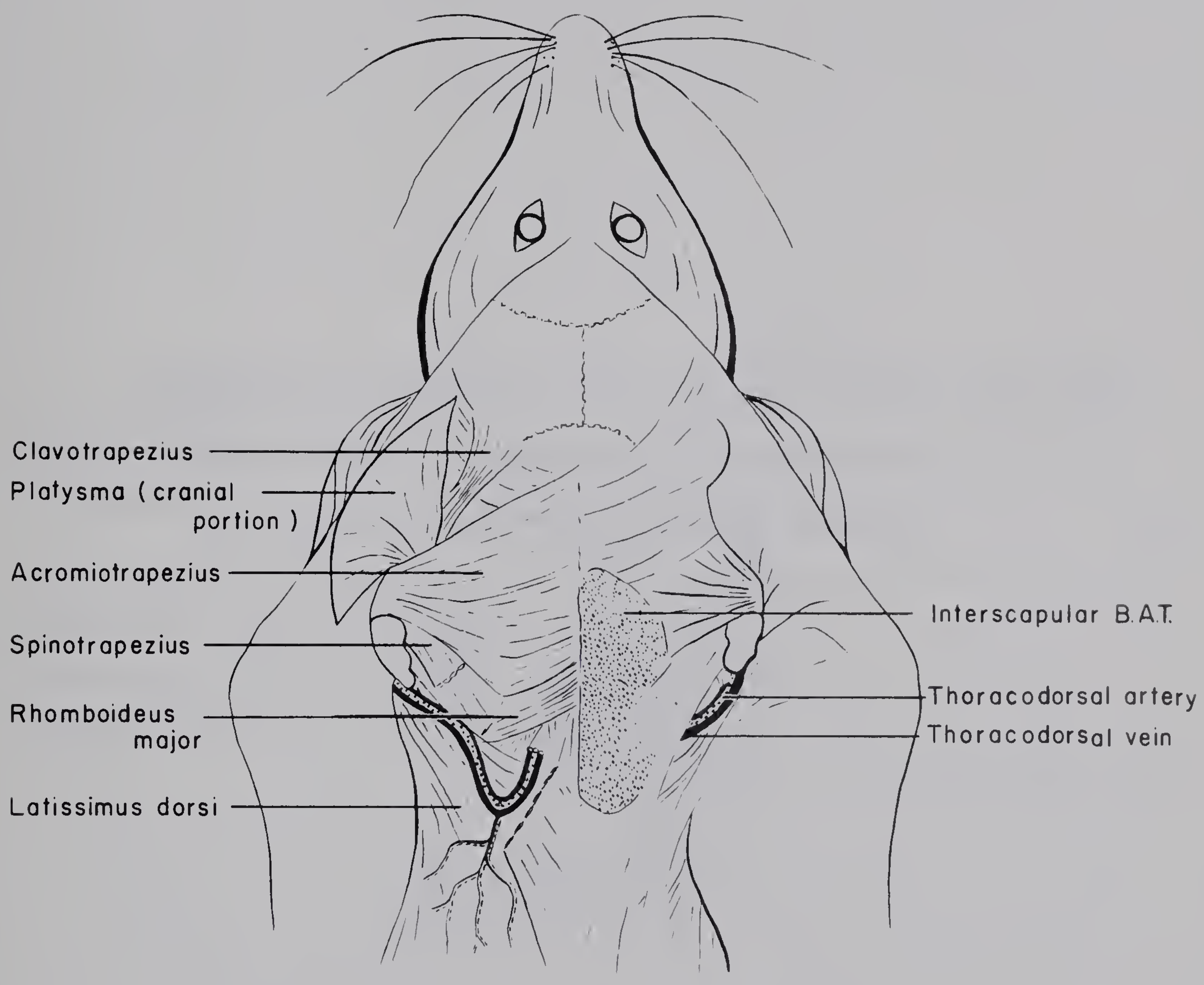

Clavotrapezius
Platysma (cranial portion)
Acromiotrapezius
Spinotrapezius
Rhomboideus major
Latissimus dorsi
Interscapular B.A.T.
Thoracodorsal artery
Thoracodorsal vein

Fig. 23. Dorsal view of the neck and thorax of *Peromyscus maniculatus*. The interscapular brown adipose tissue is removed to show Sulzer's vein.

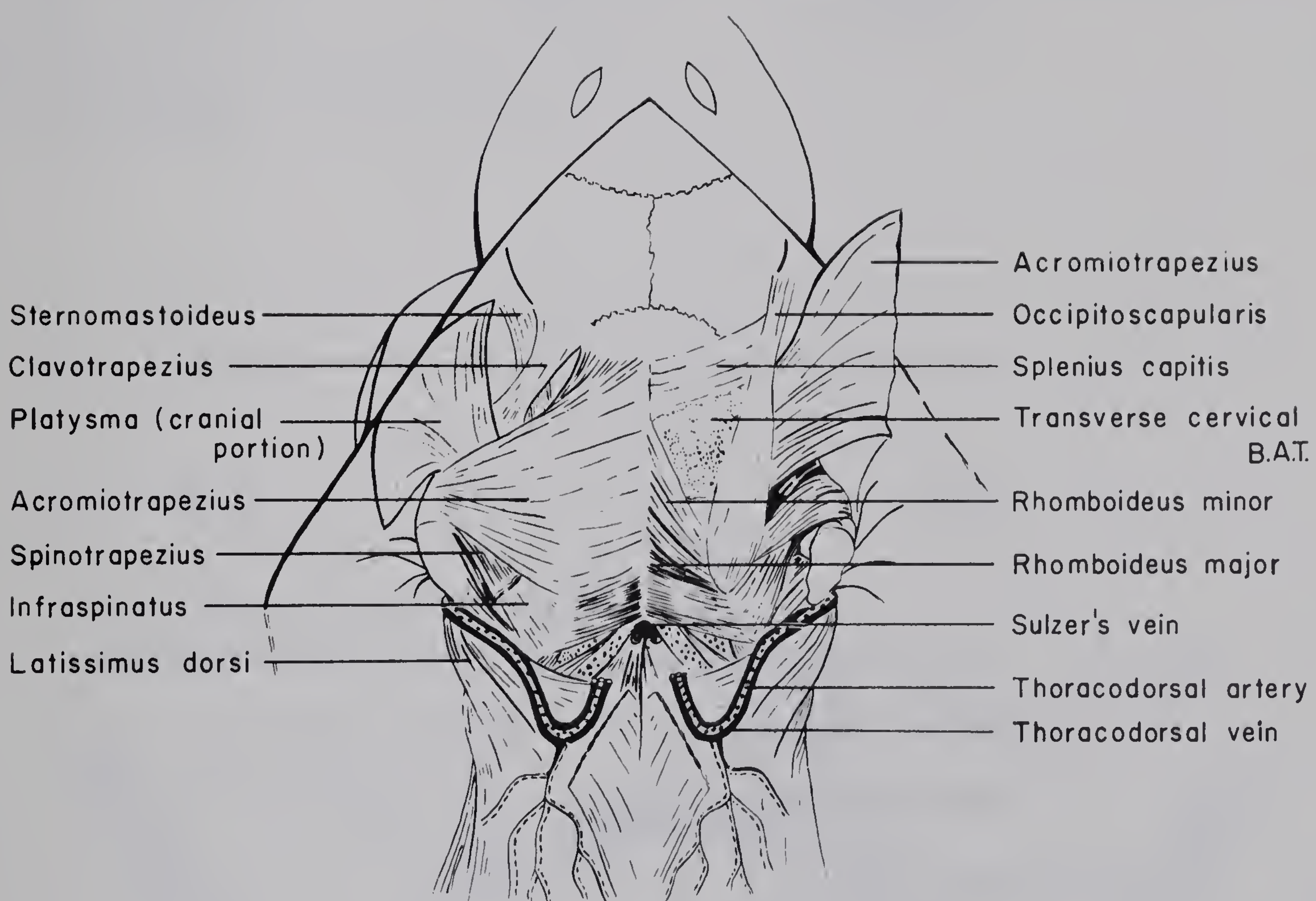
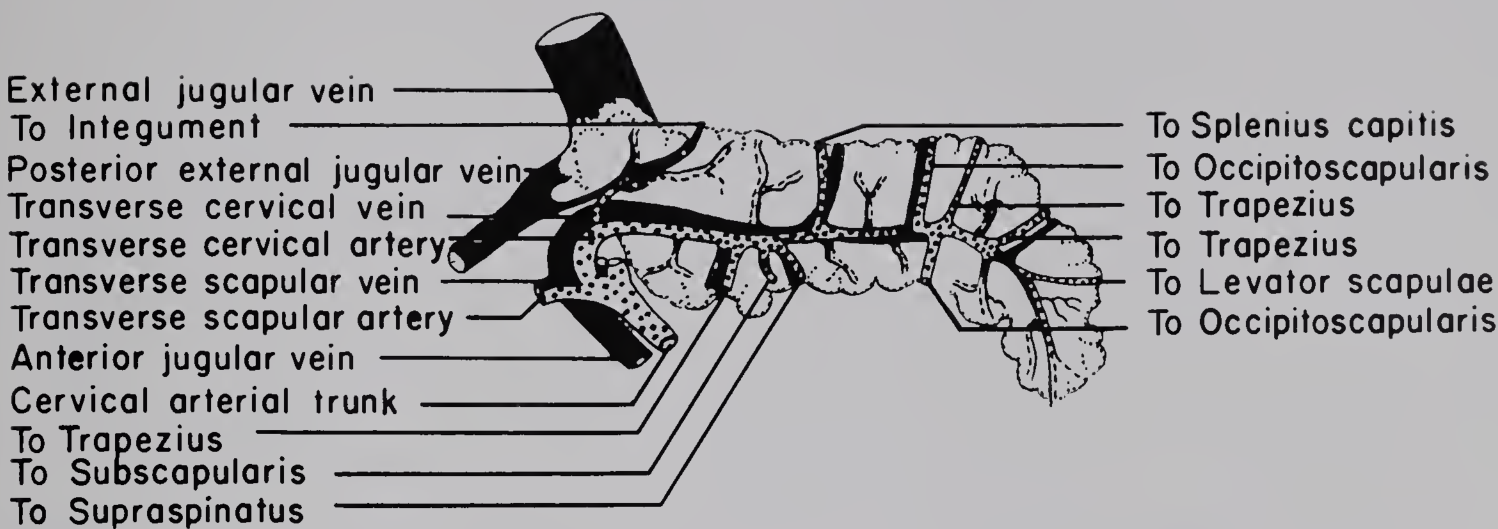
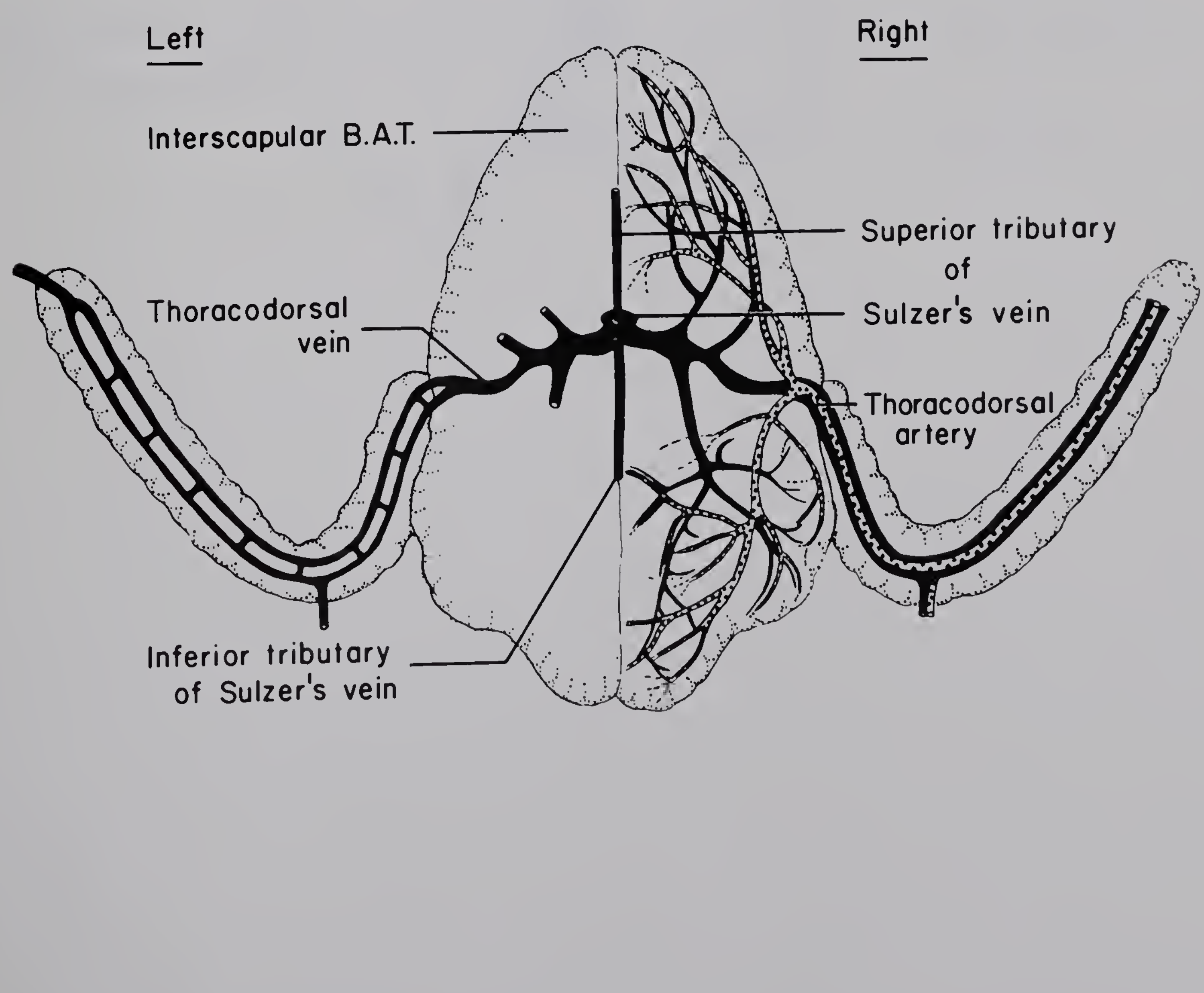

Sternomastoideus
Clavotrapezius
Platysma (cranial portion)
Acromiotrapezius
Spinotrapezius
Infraspinatus
Latissimus dorsi
Acromiotrapezius
Occipitoscapularis
Splenius capitis
Transverse cervical B.A.T.
Rhomboideus minor
Rhomboideus major
Sulzer's vein
Thoracodorsal artery
Thoracodorsal vein

Fig. 24. A diagramatic representation of the relationship between the blood vascular system and the transverse cervical brown fat deposit of *Peromyscus maniculatus*.

Fig. 25. A diagramatic representation of the vascularization of the interscapular brown adipose tissue of *Peromyscus maniculatus*.



External jugular vein
To Integument
Posterior external jugular vein
Transverse cervical vein
Transverse cervical artery
Transverse scapular vein
Transverse scapular artery
Anterior jugular vein
Cervical arterial trunk
To Trapezius
To Subscapularis
To Supraspinatus
To Splenius capitis
To Occipitoscapularis
To Trapezius
To Trapezius
To Levator scapulae
To Occipitoscapularis



Left
Right
Interscapular B.A.T.
Superior tributary of Sulzer's vein
Thoracodorsal vein
Thoracodorsal artery
Inferior tributary of Sulzer's vein

Fig. 26. Diagram of the venous shunt system of the interscapular brown fat deposit of *Peromyscus maniculatus*.

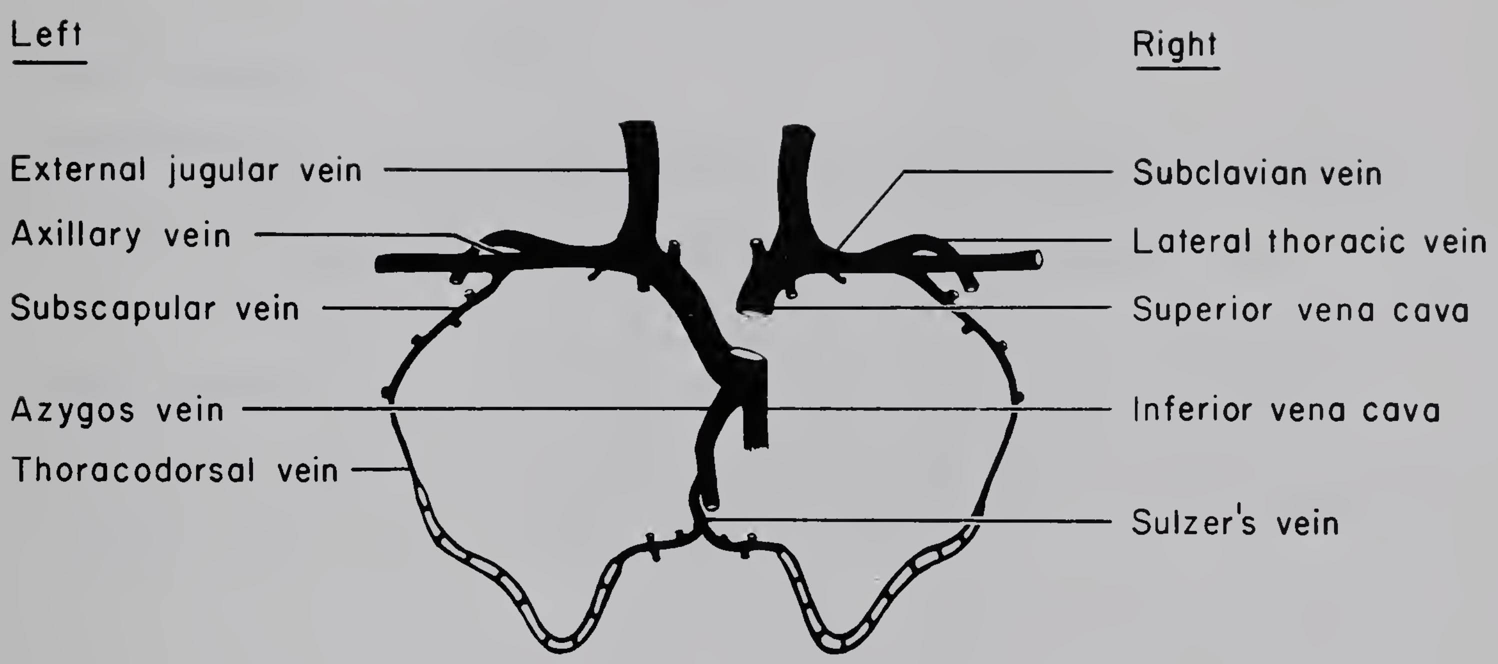
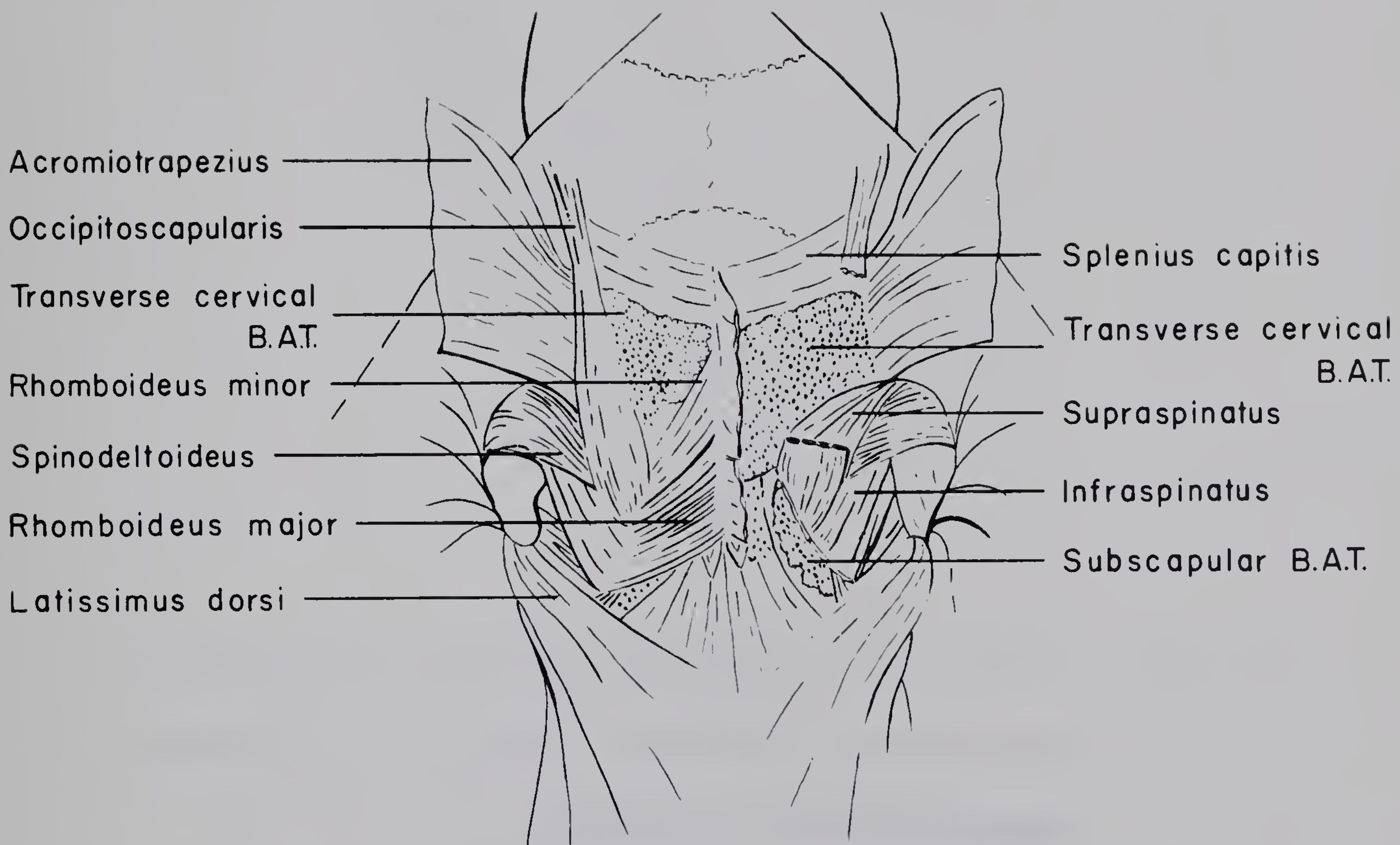

Left
Right
External jugular vein
Axillary vein
Subscapular vein
Azygos vein
Thoracodorsal vein
Subclavian vein
Lateral thoracic vein
Superior vena cava
Inferior vena cava
Sulzer's vein

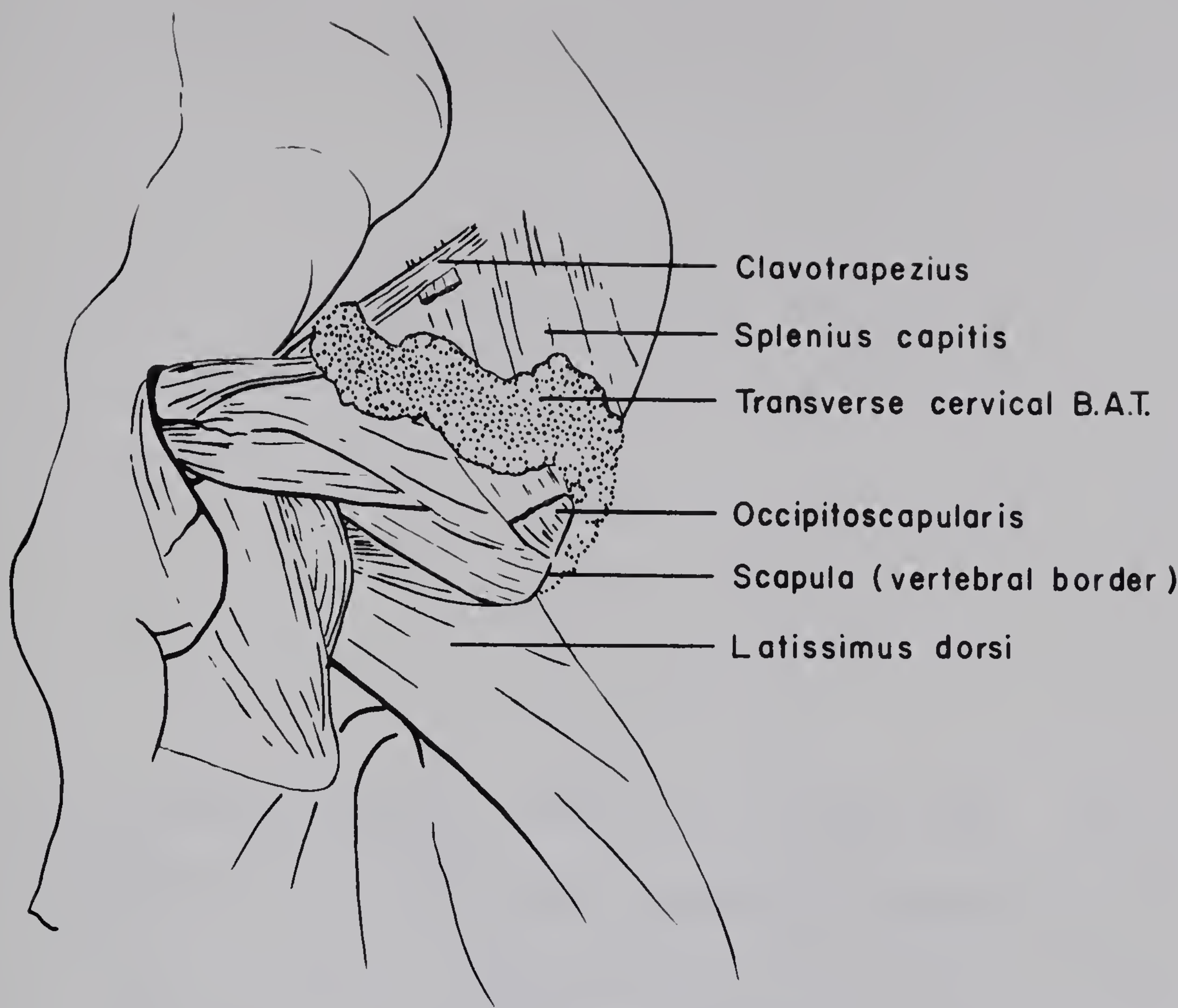
Fig. 27. Dorsal view of the transverse cervical brown adipose tissue of *Peromyscus maniculatus*.



Acromiotrapezius
Occipitoscapularis
Transverse cervical B.A.T.
Rhomboideus minor
Spinodeltoideus
Rhomboideus major
Latissimus dorsi
Splenius capitis
Transverse cervical B.A.T.
Supraspinatus
Infraspinatus
Subscapular B.A.T.

Fig. 28. Lateral view of the left transverse cervical brown fat deposit of *Peromyscus maniculatus*.

Fig. 29. Lateral view of the anterior trunk of *Peromyscus maniculatus*. The severed ends of the transverse cervical vessels are shown.


Clavotrapezius
Splenius capitis
Transverse cervical B.A.T.
Occipitoscapularis
Scapula (vertebral border)
Latissimus dorsi

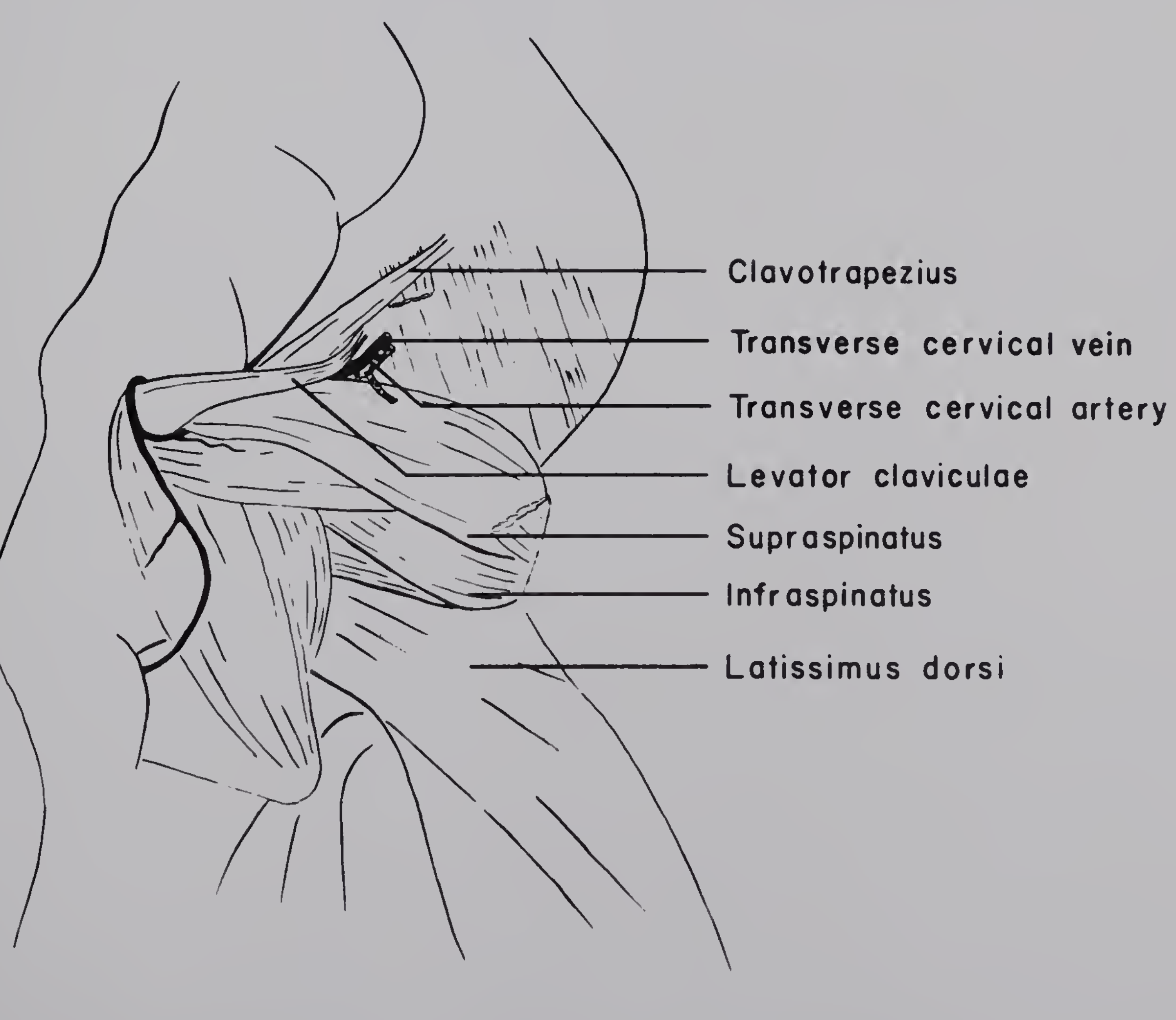
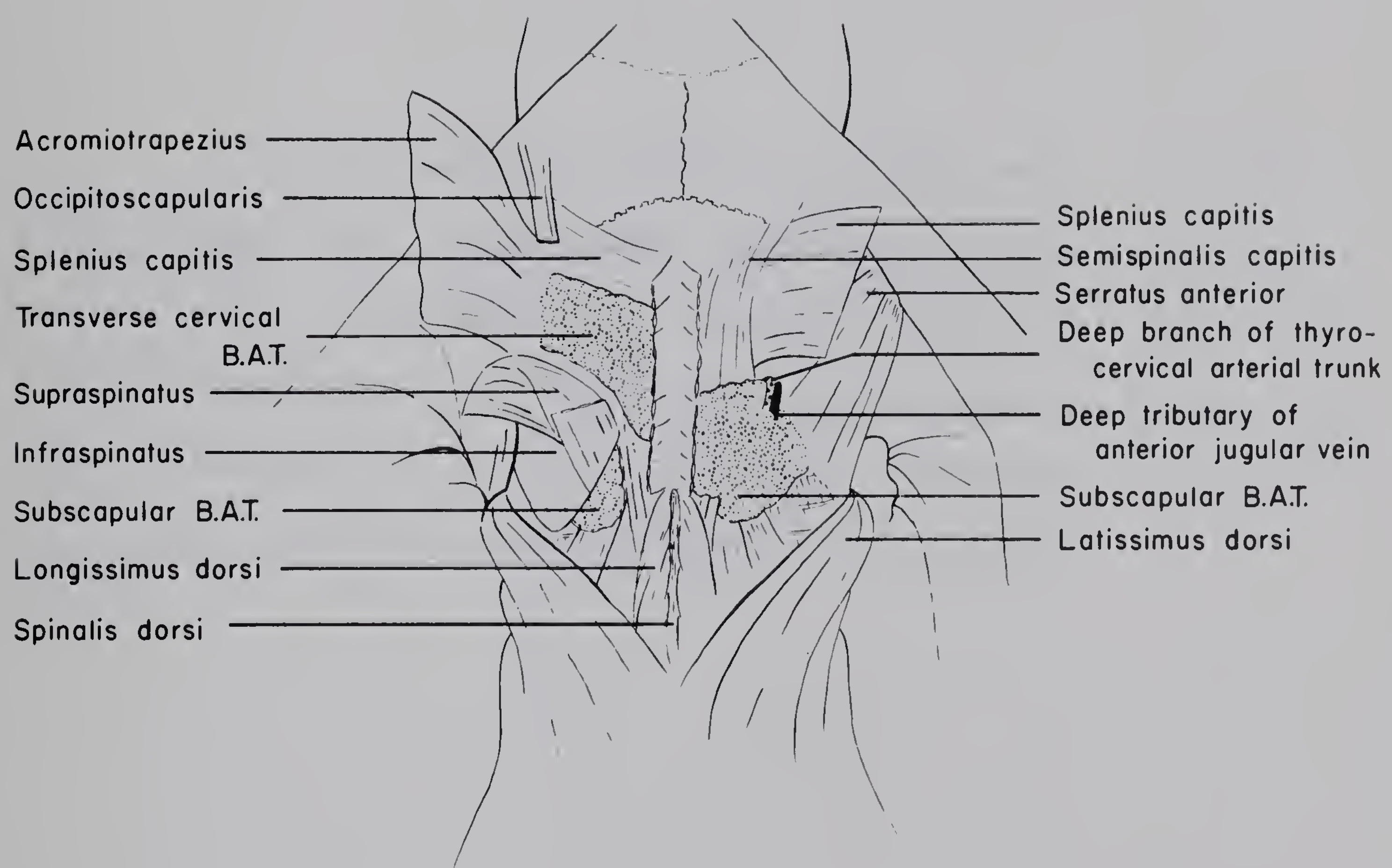
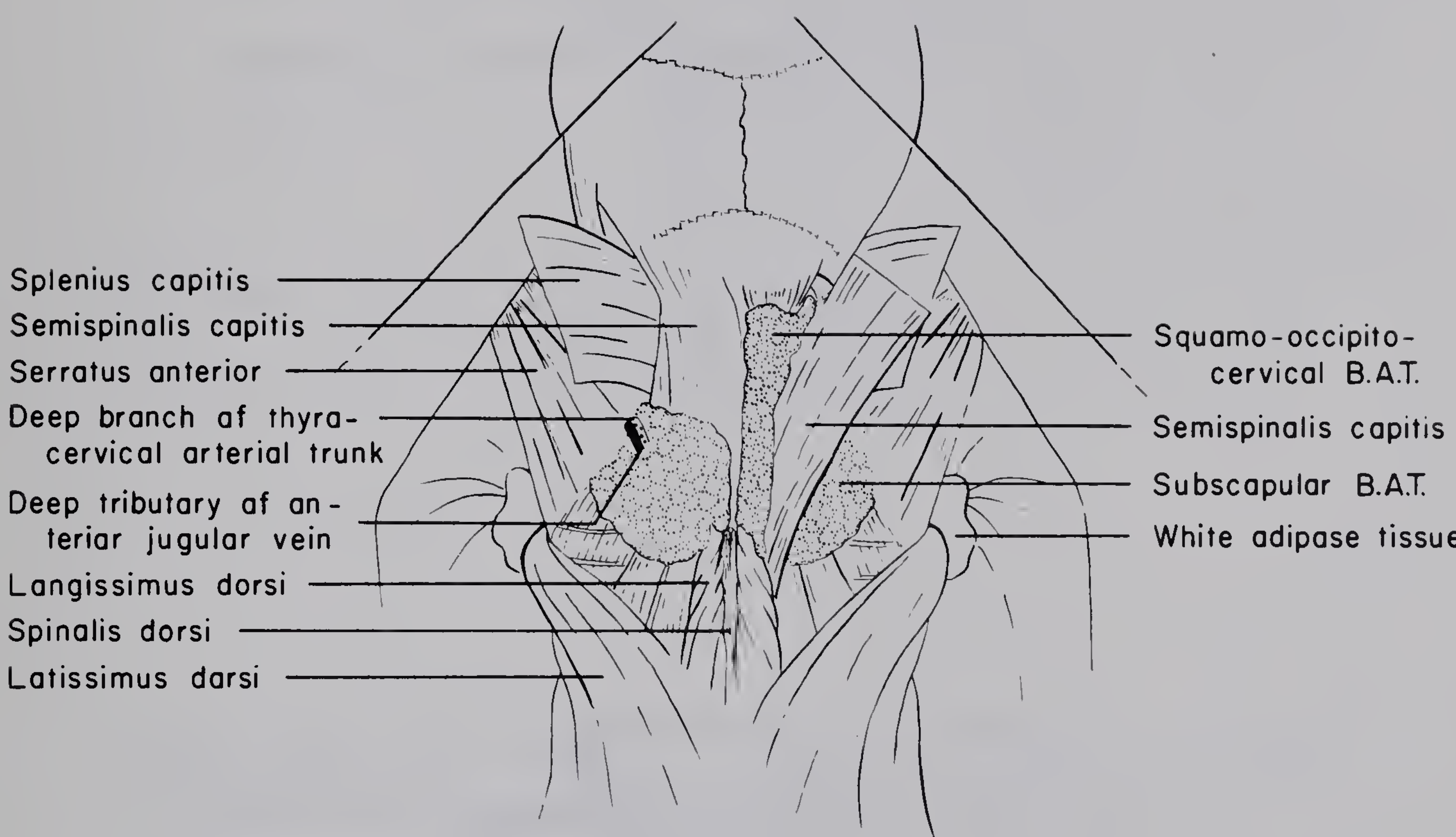

Clavotrapezius
Transverse cervical vein
Transverse cervical artery
Levator claviculae
Supraspinatus
Infraspinatus
Latissimus dorsi

Fig. 30. Deep aspect of the dorsal neck and thoracic region of *Peromyscus maniculatus*. The right scapula is rotated ventrally so as to reveal the subscapular brown fat deposit. The blood vessels, which supply and drain this tissue, are shown.



Acromiotrapezius
Occipitoscapularis
Splenius capitis
Transverse cervical B.A.T.
Supraspinatus
Infraspinatus
Subscapular B.A.T.
Longissimus dorsi
Spinalis dorsi
Splenius capitis
Semispinalis capitis
Serratus anterior
Deep branch of thyro-cervical arterial trunk
Deep tributary of anterior jugular vein
Subscapular B.A.T.
Latissimus dorsi

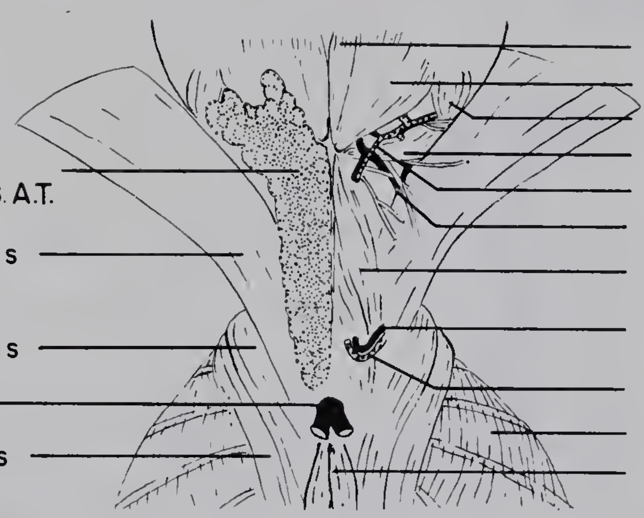
Fig. 31. Deep aspect of the dorsal neck and thoracic region of *Peromyscus maniculatus*. Each scapula is rotated ventrally so as to reveal the subscapular brown fat deposits. The right *Semispinalis capitis* is cut to reveal the squamo-occipito-cervical brown fat deposit of this side.



Splenius capitis
Semispinalis capitis
Serratus anterior
Deep branch af thyra-cervical arterial trunk
Deep tributary af an-teriar jugular vein
Langissimus dorsi
Spinalis dorsi
Latissimus darsi
Squamo-occipito-cervical B.A.T.
Semispinalis capitis
Subscapular B.A.T.
White adipase tissue

Fig. 32. Deep aspect of the dorsal neck region of *Peromyscus maniculatus*. The right lobe of the squamo-occipito-cervical B.A.T. is removed to show the arteries that supply branches to this tissue and the veins that receive tributaries from it.

Fig. 33. A diagramatic representation of the origin of the left deep cervical artery *(Profunda cervicalis)* and the termination of the posterior cervical tributary of the right superior intercostal vein of *Peromyscus maniculatus*.


Rectus capitis posterior minor
Rectus capitis posteriar major
Obliquus capitis superiar
Obliquus capitis inferior
Occipital artery
Pasteriar auricular vein
Semispinalis cervicis
Pasterior cervical tributary of superiar intercastal vein
Prafunda cervicalis
Intercastalis externi
Spinalis dorsi
Squamo-occipito-cervical B.A.T.
Semispinalis capitis
Longissmus cervicis
Sulzer's vein
Iliocastalis cervicis

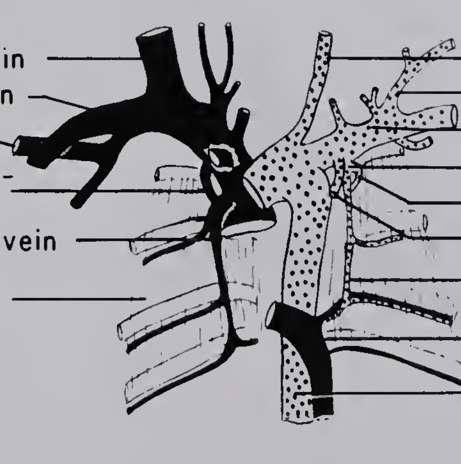
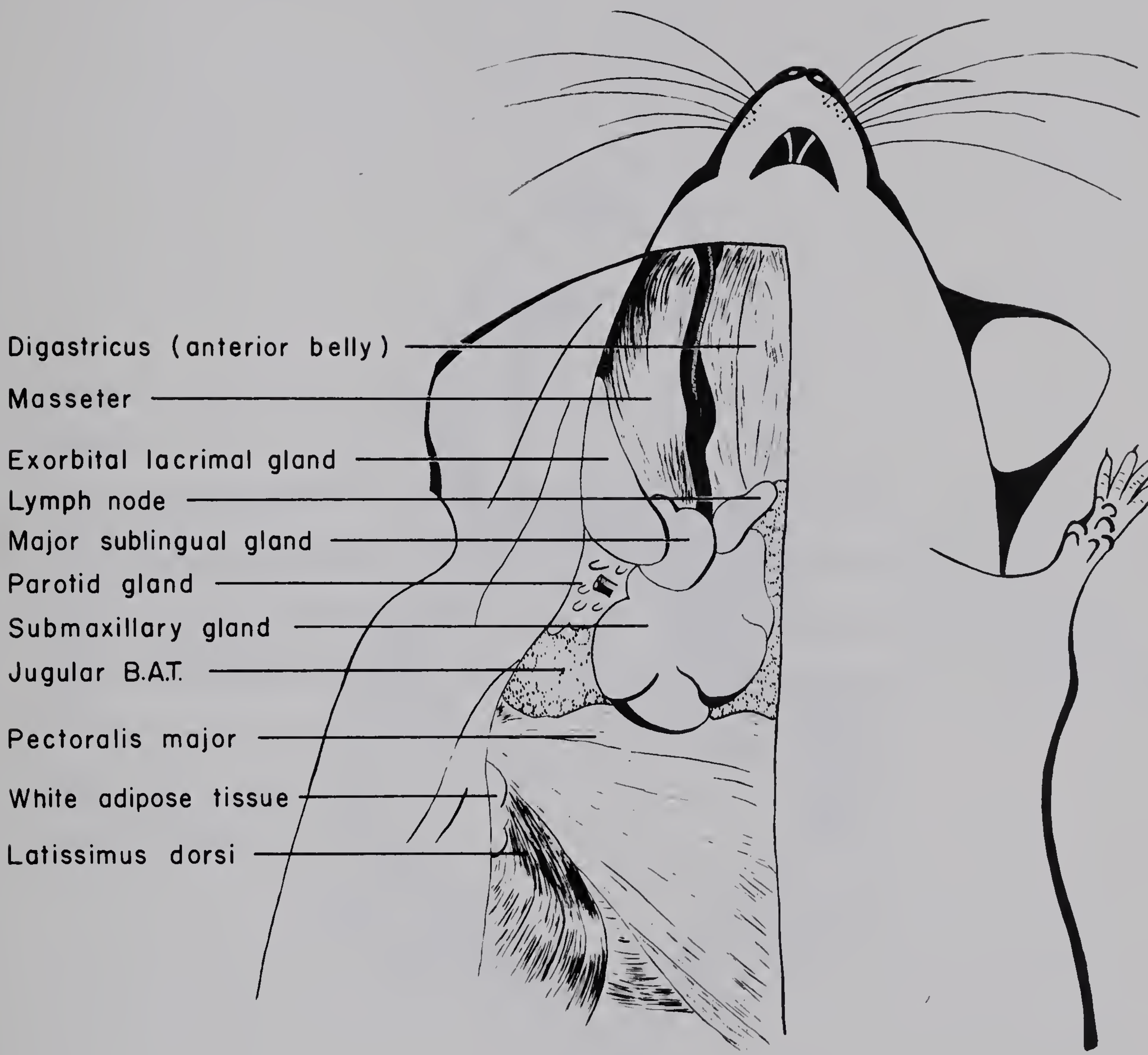

External jugular vein
Lateral tharacic vein
Axillary vein
Posterior cervical tributary af
Superiar intercastal vein
Intercastalis interni
Cammon carotid artery
Cervical arterial trunk
Subclavian artery
Costocervical arterial trunk
Profunda cervicalis
Internal mammary artery
Superior intercostal artery
Azygos vein
Dorsal aorta

Fig. 34. Ventral view of the right neck region of *Peromyscus maniculatus*. The relationship between the glands of the neck and the jugular brown adipose tissue deposit is shown.



Digastricus (anterior belly)
Masseter
Exorbital lacrimal gland
Lymph node
Major sublingual gland
Parotid gland
Submaxillary gland
Jugular B.A.T.
Pectoralis major
White adipose tissue
Latissimus dorsi

Fig. 35. Ventral view of the neck region of *Peromyscus maniculatus*. On the left side, the glands are removed to show the relationship between the jugular brown adipose tissue and the external jugular vein.

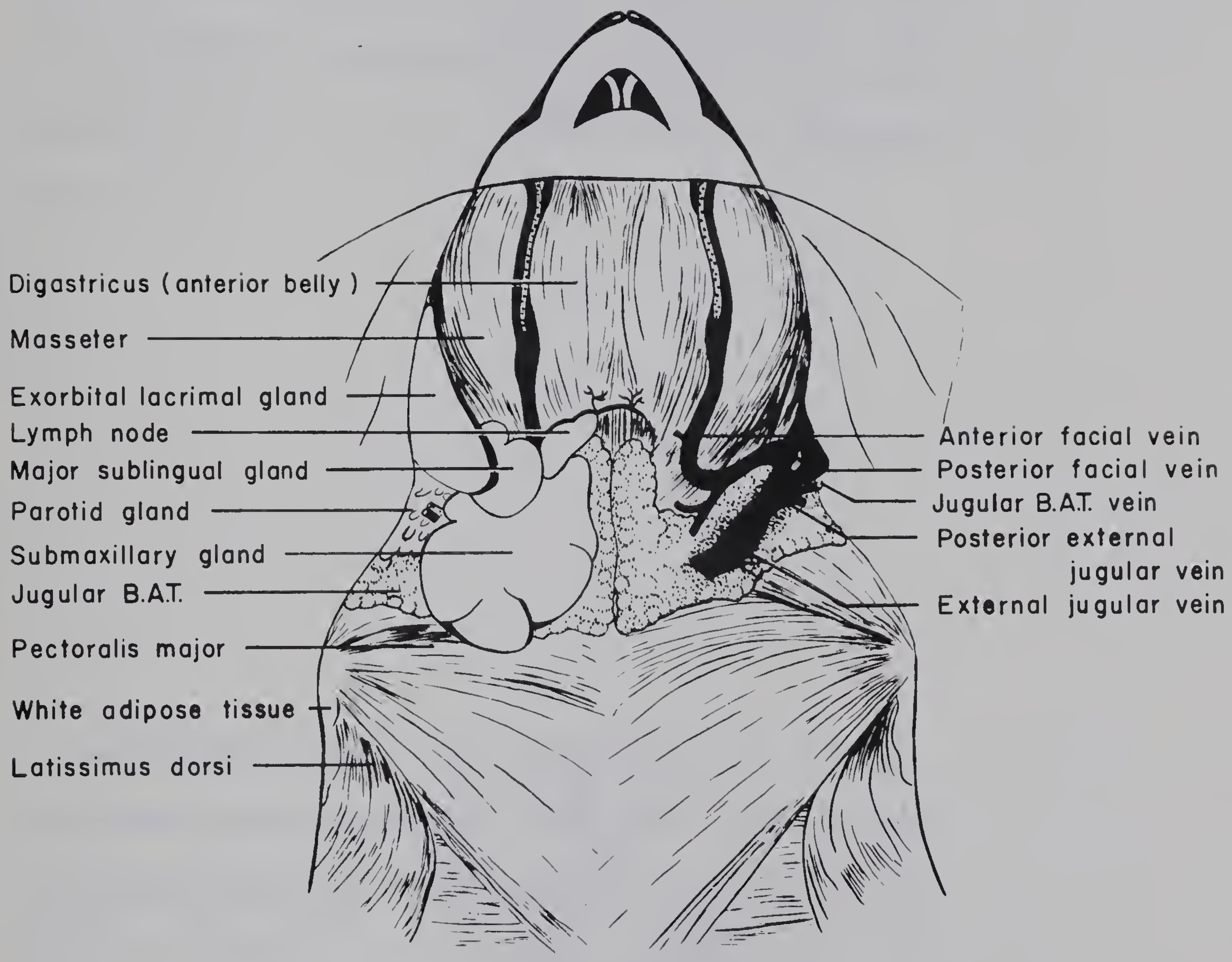
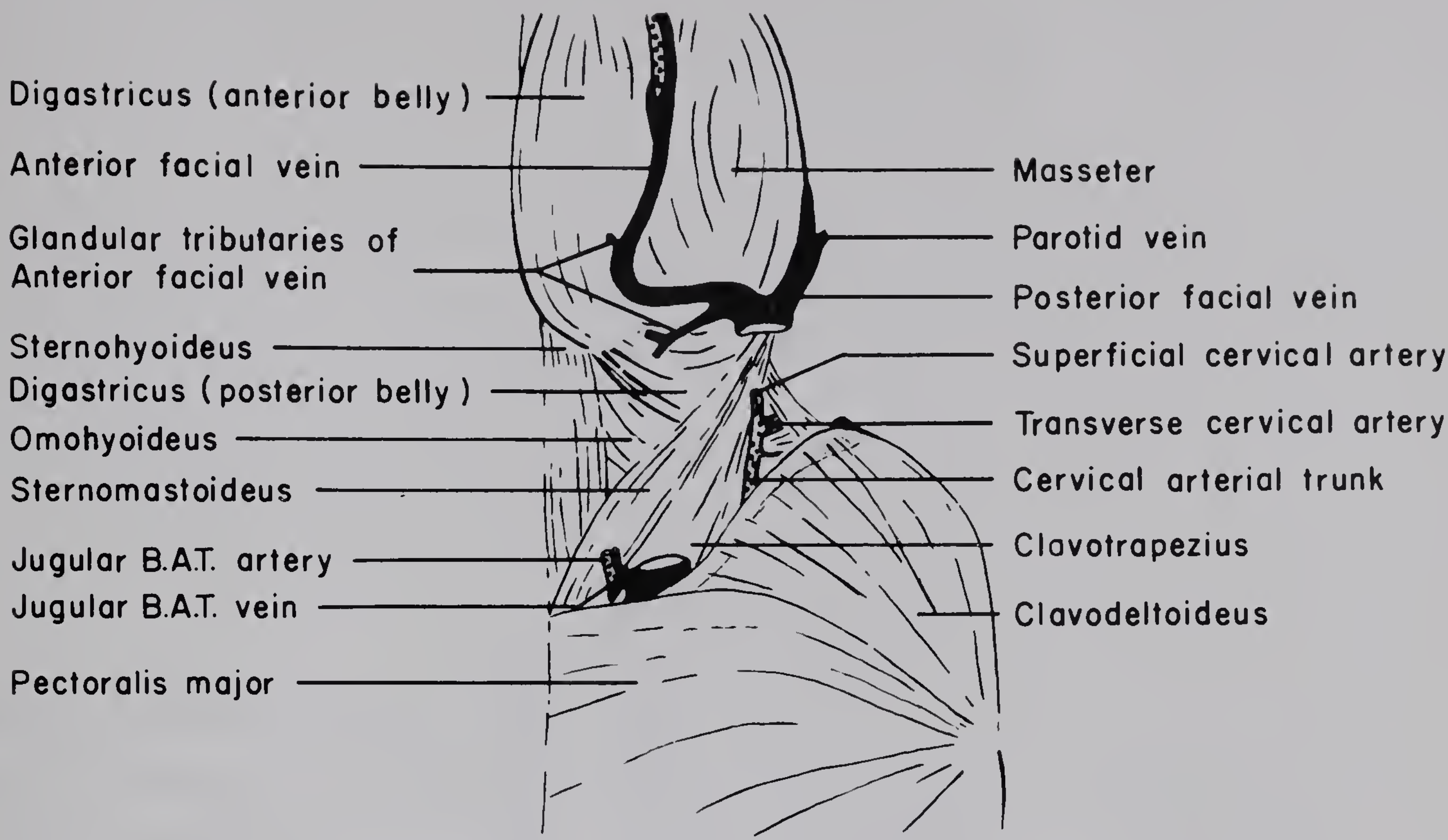
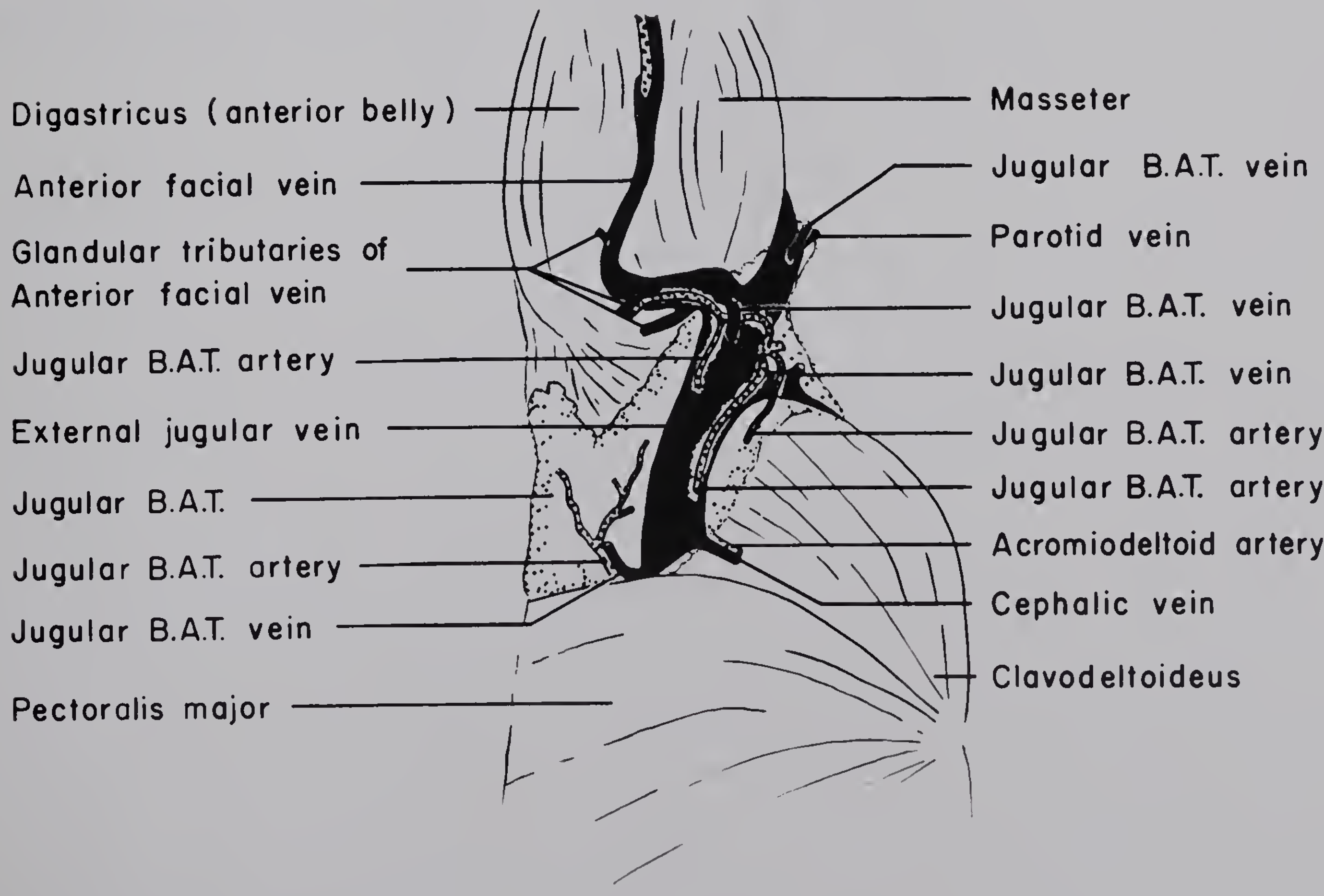

Digastricus (anterior belly)
Masseter
Exorbital lacrimal gland
Lymph node
Major sublingual gland
Parotid gland
Submaxillary gland
Jugular B.A.T.
Pectoralis major
White adipose tissue
Latissimus dorsi
Anterior facial vein
Posterior facial vein
Jugular B.A.T. vein
Posterior external jugular vein
External jugular vein

Fig. 36. Ventral view of the left neck region of *Peromyscus maniculatus*. The origin of the left transverse cervical artery and its relationship to adjacent structures is shown.

Fig. 37. Ventral view of the left neck region of *Peromyscus maniculatus*. The blood vessels which supply and drain the left jugular brown adipose tissue deposit are illustrated.



Digastricus (anterior belly)
Anterior facial vein
Glandular tributaries of Anterior facial vein
Sternohyoideus
Digastricus (posterior belly)
Omohyoideus
Sternomastoideus
Jugular B.A.T. artery
Jugular B.A.T. vein
Pectoralis major
Masseter
Parotid vein
Posterior facial vein
Superficial cervical artery
Transverse cervical artery
Cervical arterial trunk
Clavotrapezius
Clavodeltoideus



Digastricus (anterior belly)
Anterior facial vein
Glandular tributaries of Anterior facial vein
Jugular B.A.T. artery
External jugular vein
Jugular B.A.T.
Jugular B.A.T. artery
Jugular B.A.T. vein
Pectoralis major
Masseter
Jugular B.A.T. vein
Parotid vein
Jugular B.A.T. vein
Jugular B.A.T. vein
Jugular B.A.T. artery
Jugular B.A.T. artery
Acromiodeltoid artery
Cephalic vein
Clavodeltoideus

Fig. 38. Ventral view of the left axillary region of *Peromyscus maniculatus*. The superficial aspect of the left axillary brown fat deposit is shown.

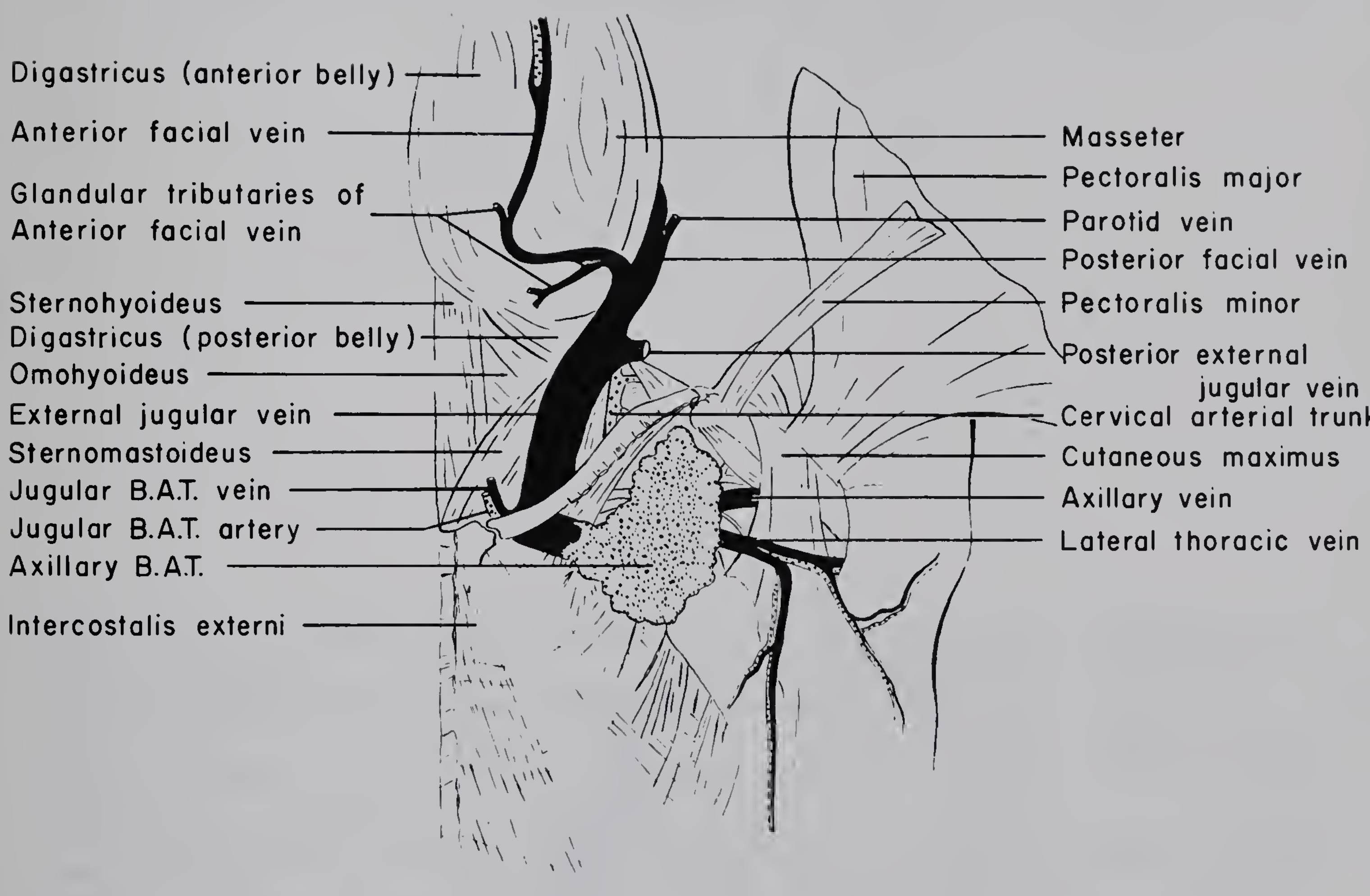

Digastricus (anterior belly)
Anterior facial vein
Glandular tributaries of Anterior facial vein
Sternohyoideus
Digastricus (posterior belly)
Omohyoideus
External jugular vein
Sternomastoideus
Jugular B.A.T. vein
Jugular B.A.T. artery
Axillary B.A.T.
Intercostalis externi
Masseter
Pectoralis major
Parotid vein
Posterior facial vein
Pectoralis minor
Posterior external jugular vein
Cervical arterial trunk
Cutaneous maximus
Axillary vein
Lateral thoracic vein

Fig. 39. Ventral view of the left axillary region of *Peromyscus maniculatus*. The superficial portion of the axillary brown fat is removed to reveal the veins which are surrounded by this tissue.

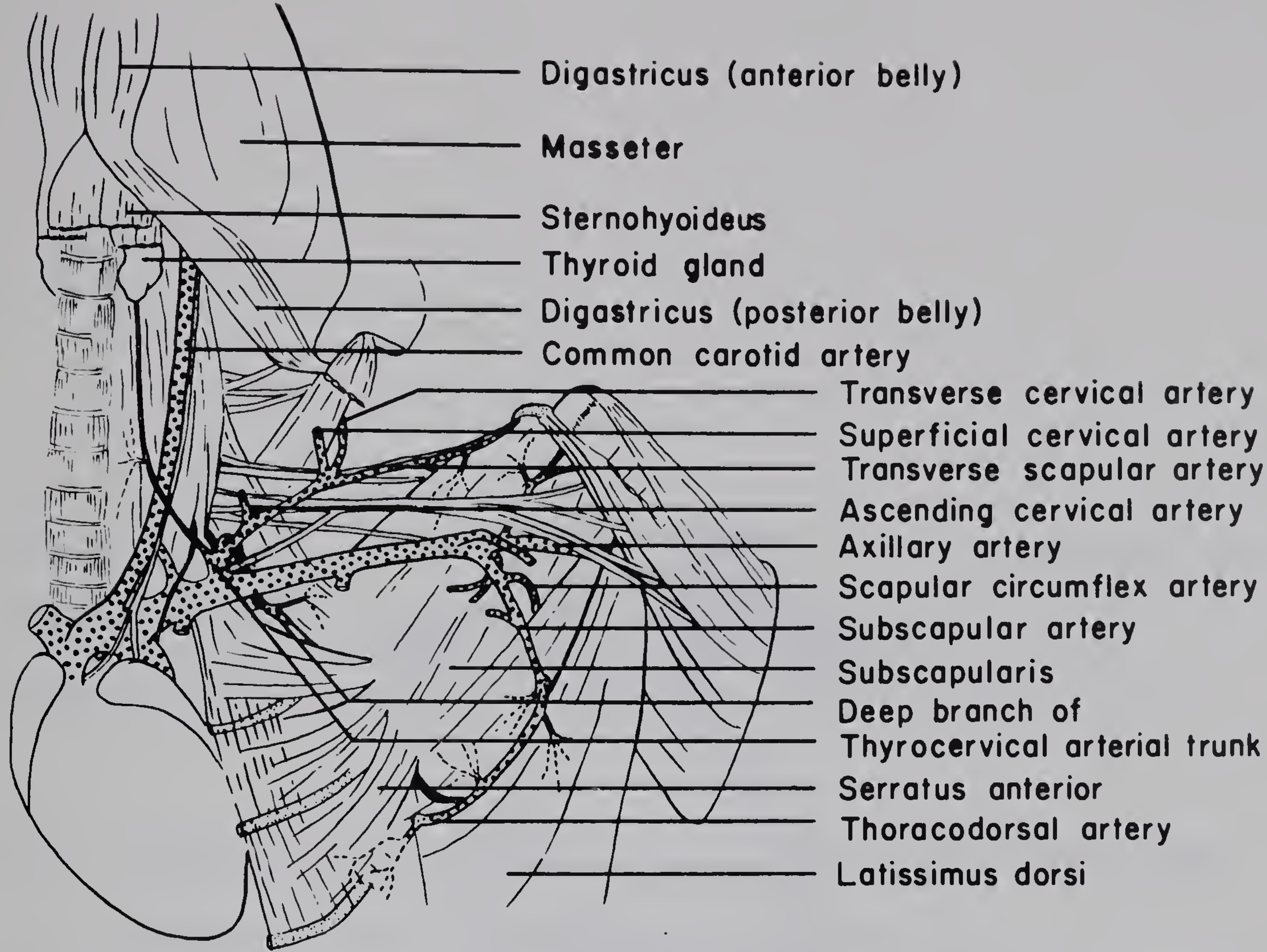
Fig. 40. Ventral view of the left axillary region of *Peromyscus maniculatus*. The superficial portion of the axillary brown fat and the veins of the axilla are removed to reveal the arteries which are surrounded by the axillary brown adipose tissue.


Anterior facial vein
Glandular tributaries of
Anterior facial vein
Sternohyoideus
Digastricus (posterior belly)
Omohyaideus
Sternamastoideus
External jugular vein
Subclavian vein
Pectaralis majar
Paratid vein
Pasteriar facial vein
Pectaralis minor
Posteriar external
jugular vein
Cutaneaus maximus
Axillary vein
Lateral tharacic vein
Subscapular vein

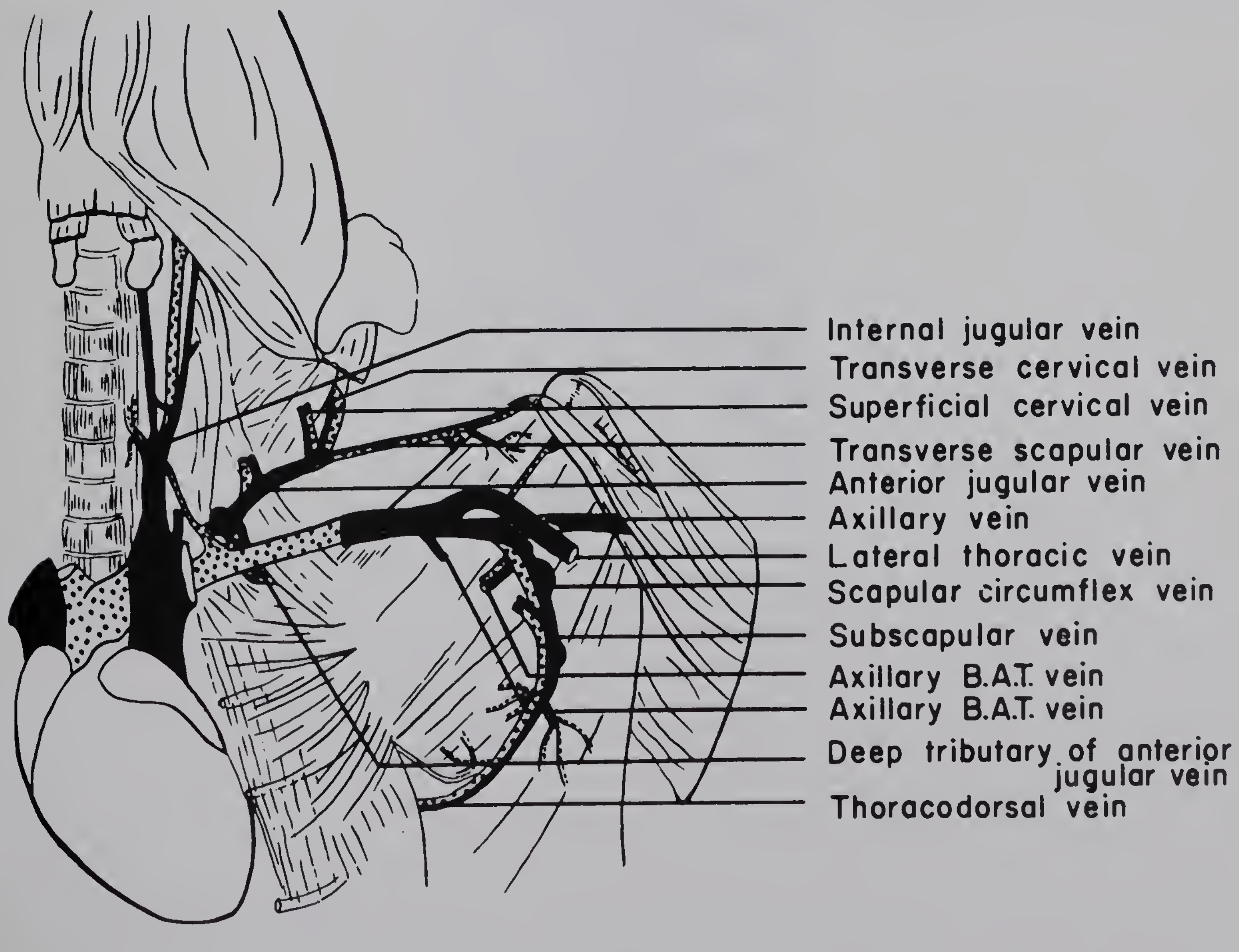

Anteriar facial vein
Glandular tributaries af
Anterior facial vein
Sternahyaideus
Digastricus (posteriar belly)
Omohyaideus
Sternomastoideus
External jugular vein
Subclavian artery
Axillary B.A.T. artery
Pectaralis majar
Paratid vein
Posterior facial vein
Pectoralis minar
Posteriar external
jugular vein
Humeral circumflex
artery
Axillary artery
Axillary B.A.T. artery
Lateral thoracic artery
Scapular circumflex
artery
Subscapular artery
Axillary B.A.T. artery

Fig. 41. Ventral view of the left neck and thoracic region of *Peromyscus maniculatus*. The shoulder girdle is abducted to reveal the origin of the deep branch of the thyrocervical arterial trunk.

Fig. 42. Ventral view of the left neck and thoracic region of *Peromyscus maniculatus*. The shoulder girdle is abducted to reveal the terminal portion of the deep tributary of the anterior jugular vein.



Digastricus (anterior belly)
Masseter
Sternohyoideus
Thyroid gland
Digastricus (posterior belly)
Common carotid artery
Transverse cervical artery
Superficial cervical artery
Transverse scapular artery
Ascending cervical artery
Axillary artery
Scapular circumflex artery
Subscapular artery
Subscapularis
Deep branch of
Thyrocervical arterial trunk
Serratus anterior
Thoracodorsal artery
Latissimus dorsi



Internal jugular vein
Transverse cervical vein
Superficial cervical vein
Transverse scapular vein
Anterior jugular vein
Axillary vein
Lateral thoracic vein
Scapular circumflex vein
Subscapular vein
Axillary B.A.T. vein
Axillary B.A.T. vein
Deep tributary of anterior jugular vein
Thoracodorsal vein

Fig. 43. Ventral view of the internal thorax of *Peromyscus maniculatus*. The pericardial, aortic, and intercostal portions of the intrathoracic brown adipose tissue are illustrated.

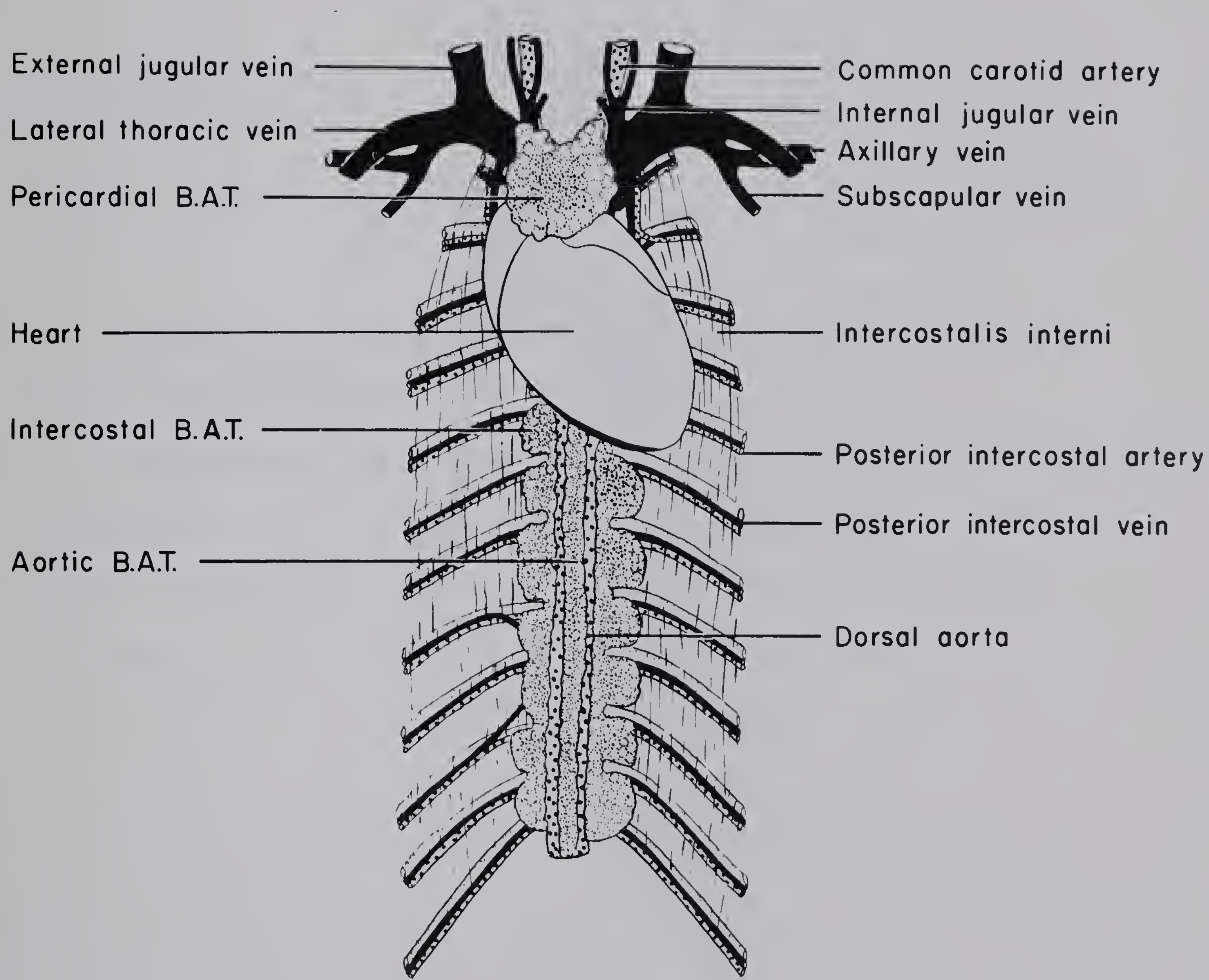

External jugular vein
Lateral thoracic vein
Pericardial B.A.T.
Heart
Intercostal B.A.T.
Aortic B.A.T.
Common carotid artery
Internal jugular vein
Axillary vein
Subscapular vein
Intercostalis interni
Posterior intercostal artery
Posterior intercostal vein
Dorsal aorta

Fig. 44. Lateral view of the internal thorax of *Peromyscus maniculatus*. The aortic, left intercostal, and inferior vena caval portions of the intrathoracic brown adipose tissue are shown.

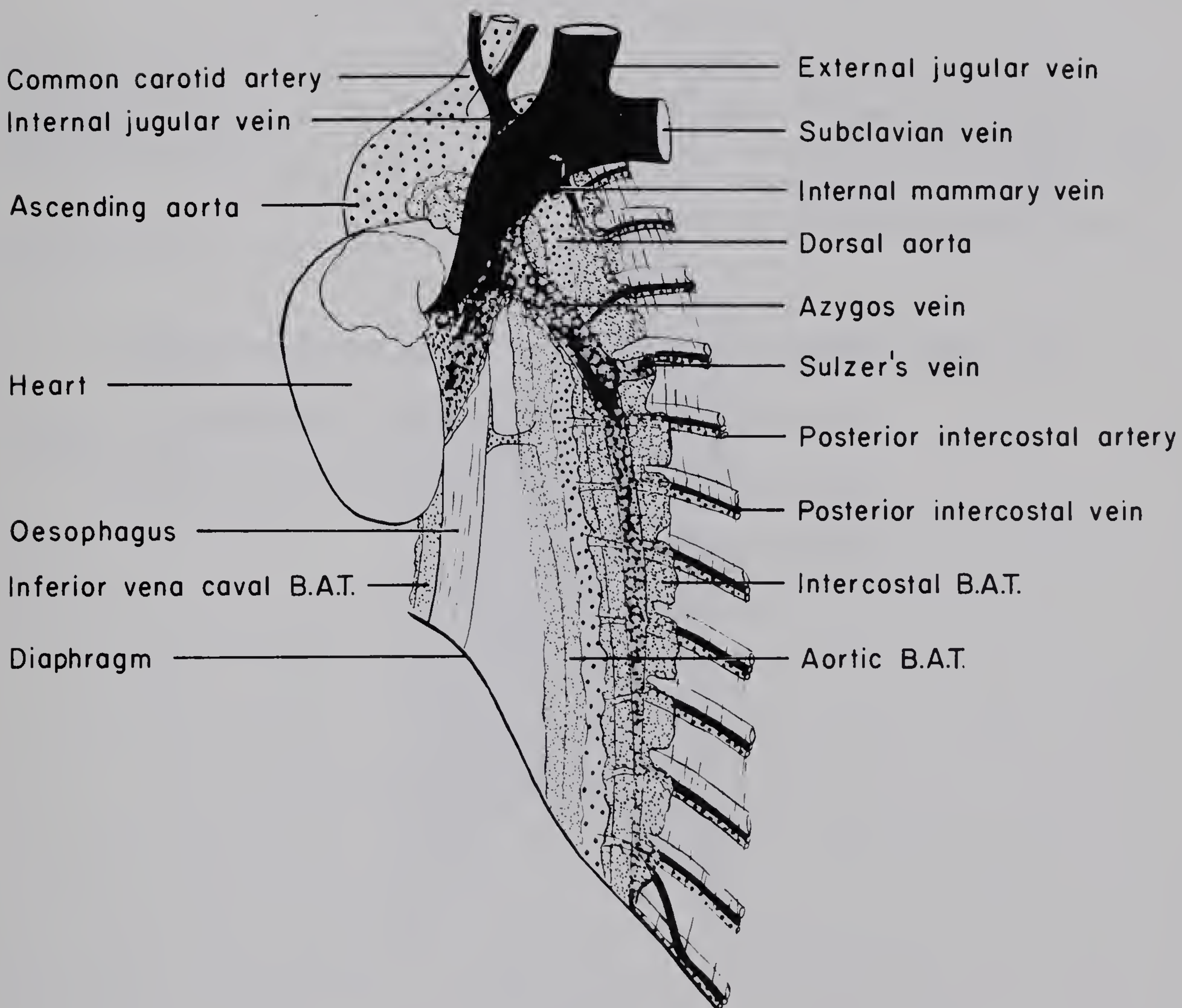

Common carotid artery
Internal jugular vein
Ascending aorta
Heart
Oesophagus
Inferior vena caval B.A.T.
Diaphragm
External jugular vein
Subclavian vein
Internal mammary vein
Dorsal aorta
Azygos vein
Sulzer's vein
Posterior intercostal artery
Posterior intercostal vein
Intercostal B.A.T.
Aortic B.A.T.

Fig. 45. Ventral view of the dorsal intrathoracic region of *Peromyscus maniculatus*. The intrathoracic brown fat is removed to demonstrate the terminal portion of Sulzer's vein.

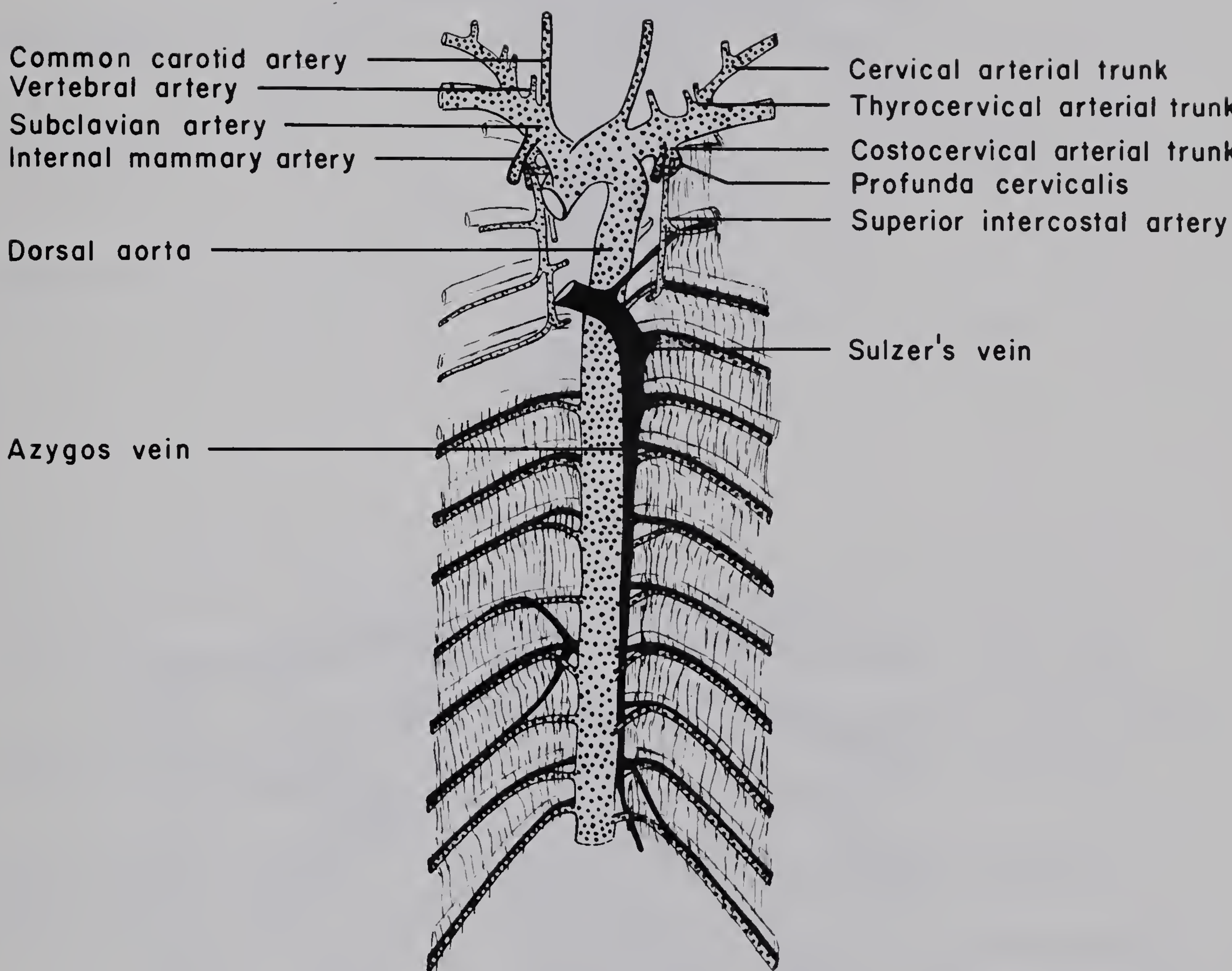
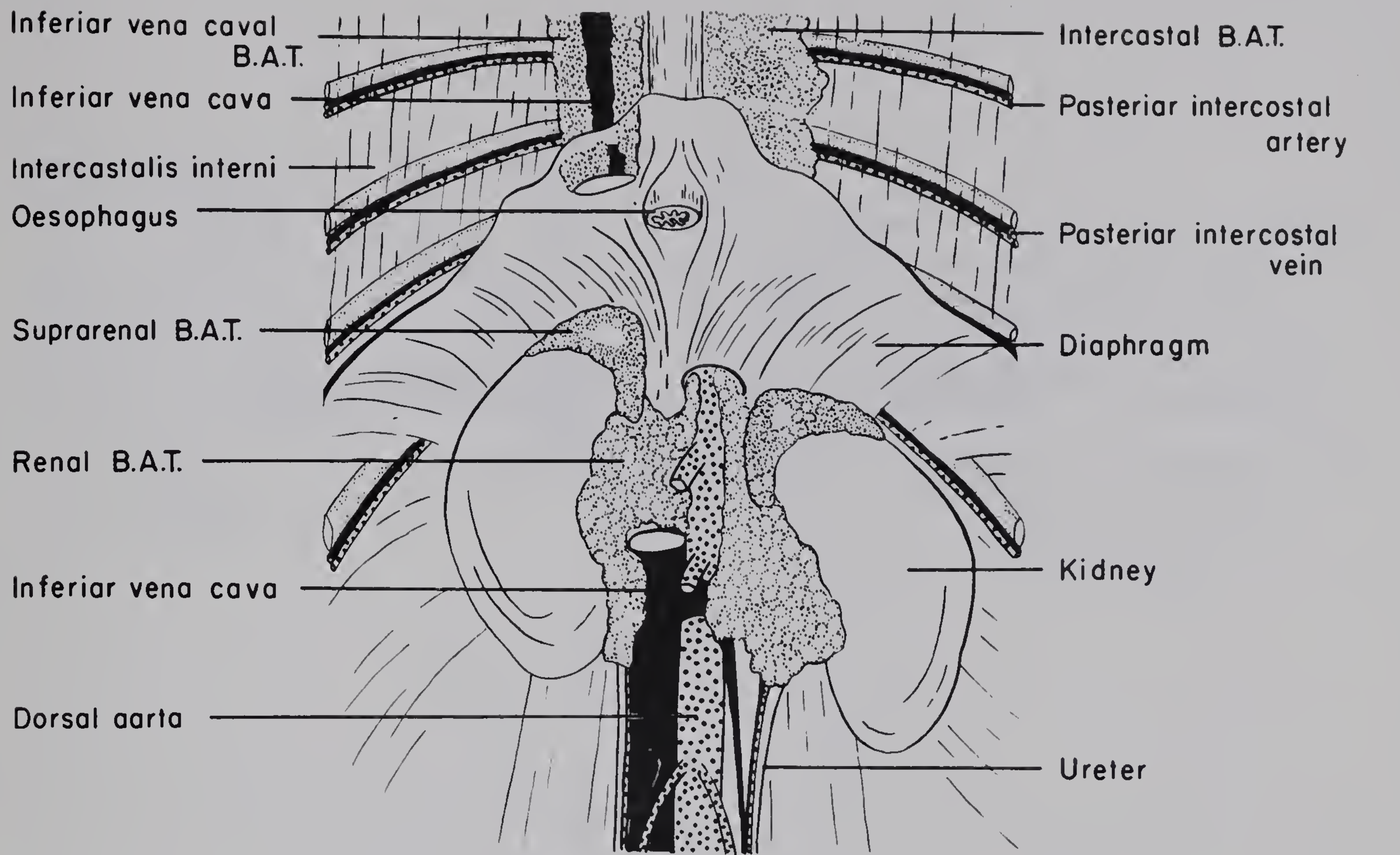

Common carotid artery
Vertebral artery
Subclavian artery
Internal mammary artery
Dorsal aorta
Azygos vein
Cervical arterial trunk
Thyrocervical arterial trunk
Costocervical arterial trunk
Profunda cervicalis
Superior intercostal artery
Sulzer's vein

Fig. 46. Ventral view of the abdominal brown adipose tissue of *Peromyscus maniculatus*.

Fig. 47. Ventral view of the kidney region of *Peromyscus maniculatus*. The abdominal brown adipose tissue is removed to reveal the relationship of this tissue to adjacent structures.


Inferiar vena caval B.A.T.
Inferiar vena cava
Intercastalis interni
Oesophagus
Suprarenal B.A.T.
Renal B.A.T.
Inferiar vena cava
Dorsal aarta
Intercastal B.A.T.
Pasteriar intercostal artery
Pasteriar intercostal vein
Diaphragm
Kidney
Ureter

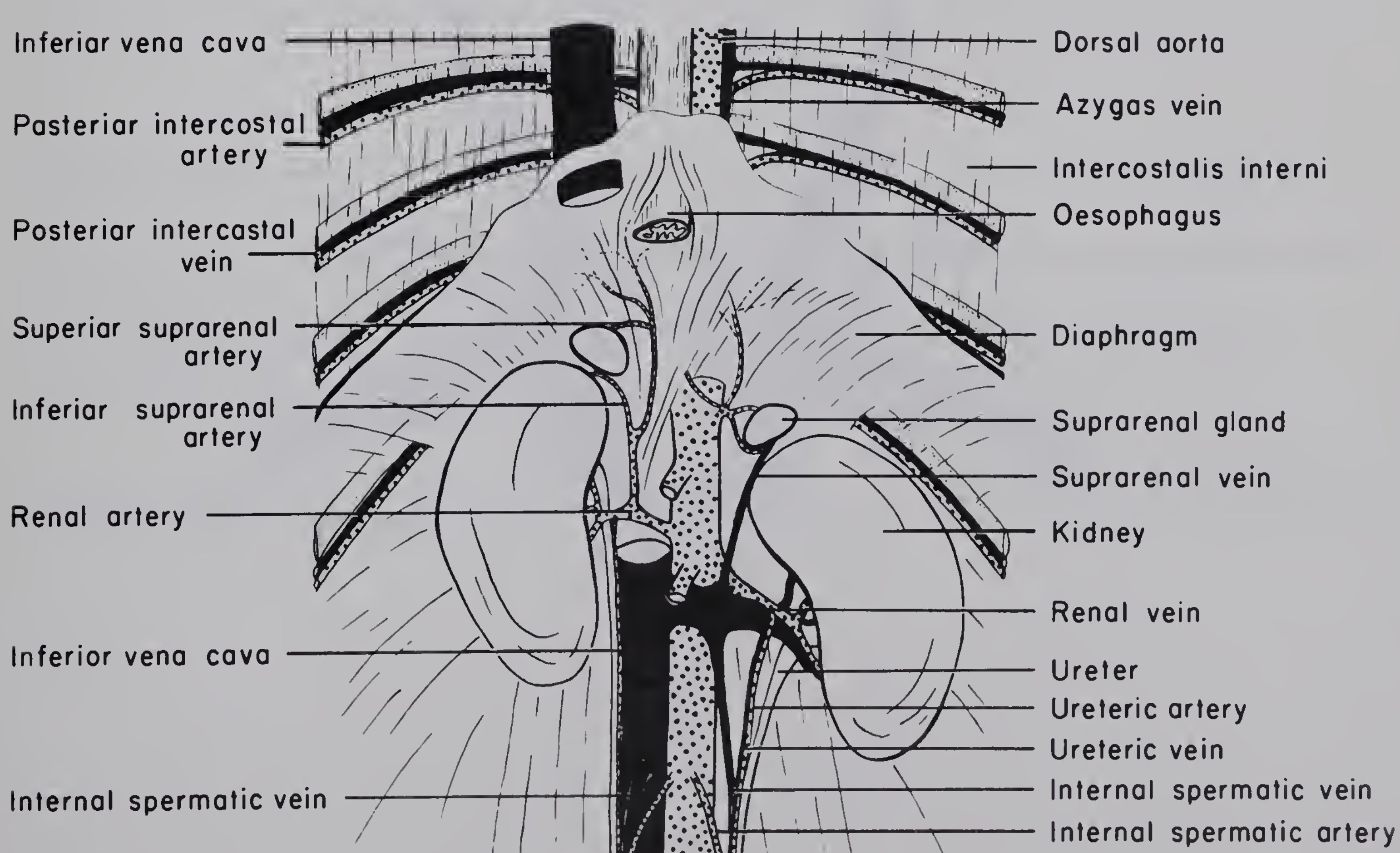
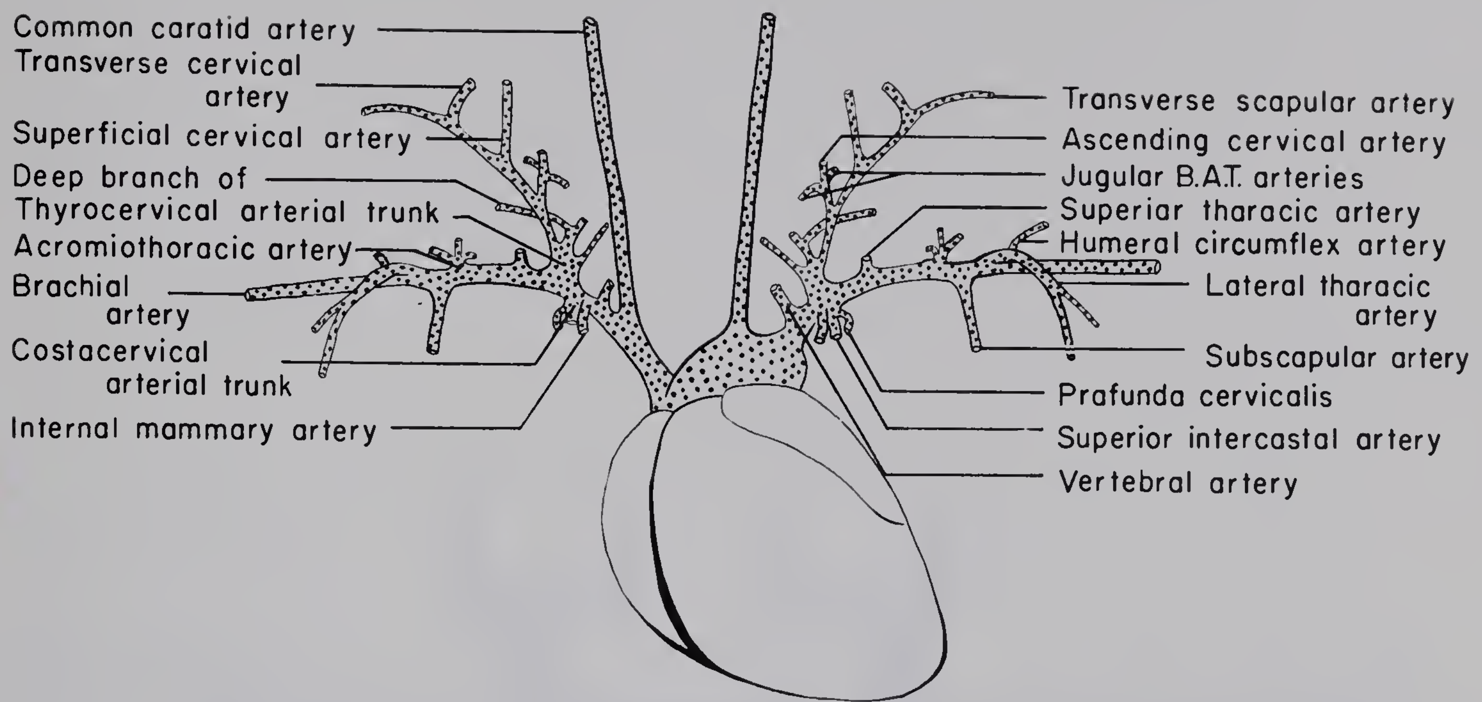

Inferiar vena cava
Pasteriar intercostal artery
Posteriar intercastal vein
Superiar suprarenal artery
Inferiar suprarenal artery
Renal artery
Inferior vena cava
Internal spermatic vein
Dorsal aorta
Azygas vein
Intercostalis interni
Oesophagus
Diaphragm
Suprarenal gland
Suprarenal vein
Kidney
Renal vein
Ureter
Ureteric artery
Ureteric vein
Internal spermatic vein
Internal spermatic artery

Fig. 48. Diagram of the origin of the major anterior arteries of *Peromyscus maniculatus*.

Fig. 49. Diagram of the terminations of the major anterior veins of *Peromyscus maniculatus*.


Common caratid artery
Transverse cervical artery
Superficial cervical artery
Deep branch of
Thyrocervical arterial trunk
Acromiothoracic artery
Brachial artery
Costacervical arterial trunk
Internal mammary artery
Transverse scapular artery
Ascending cervical artery
Jugular B.A.T. arteries
Superiar tharacic artery
Humeral circumflex artery
Lateral tharacic artery
Subscapular artery
Prafunda cervicalis
Superior intercastal artery
Vertebral artery

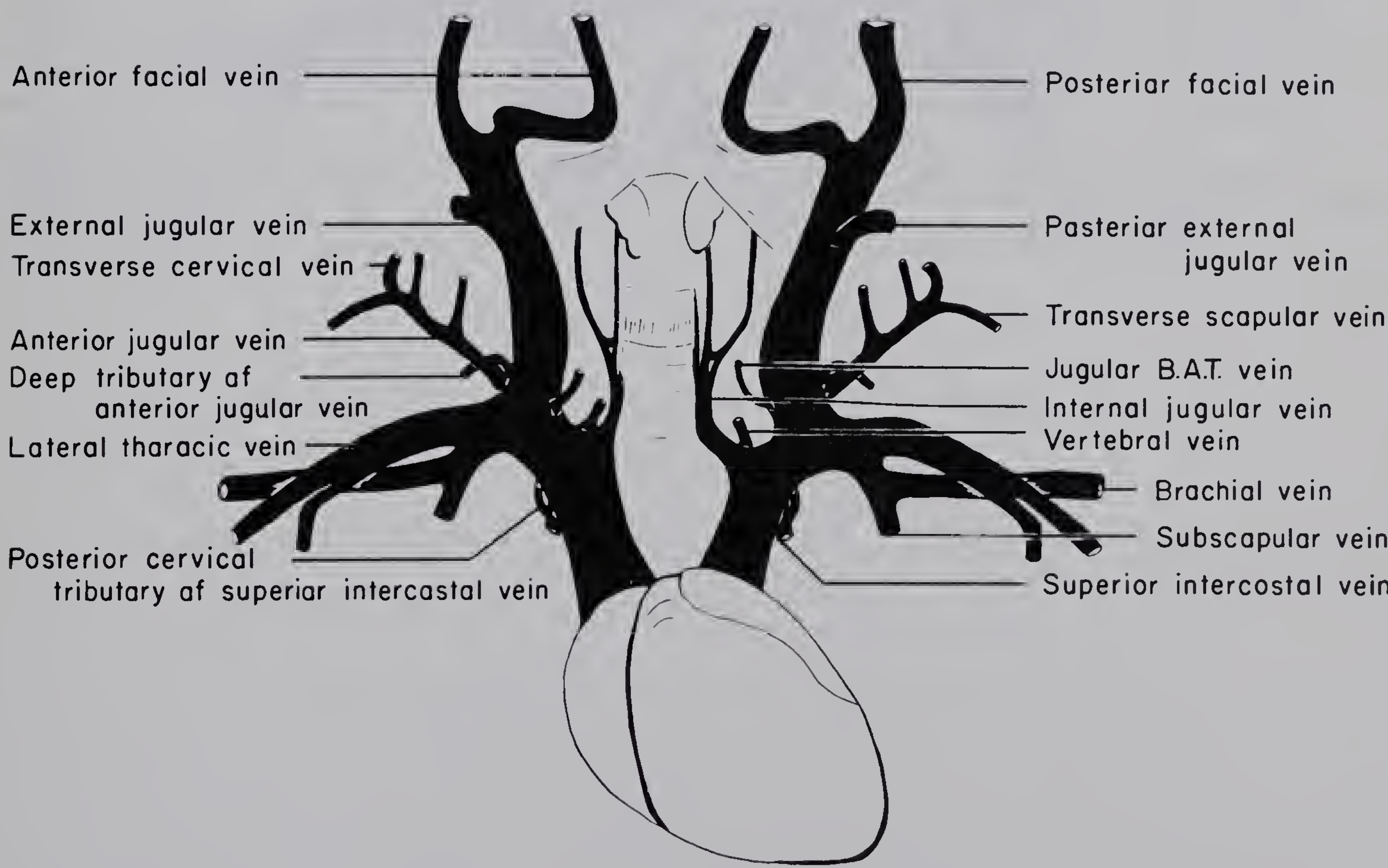
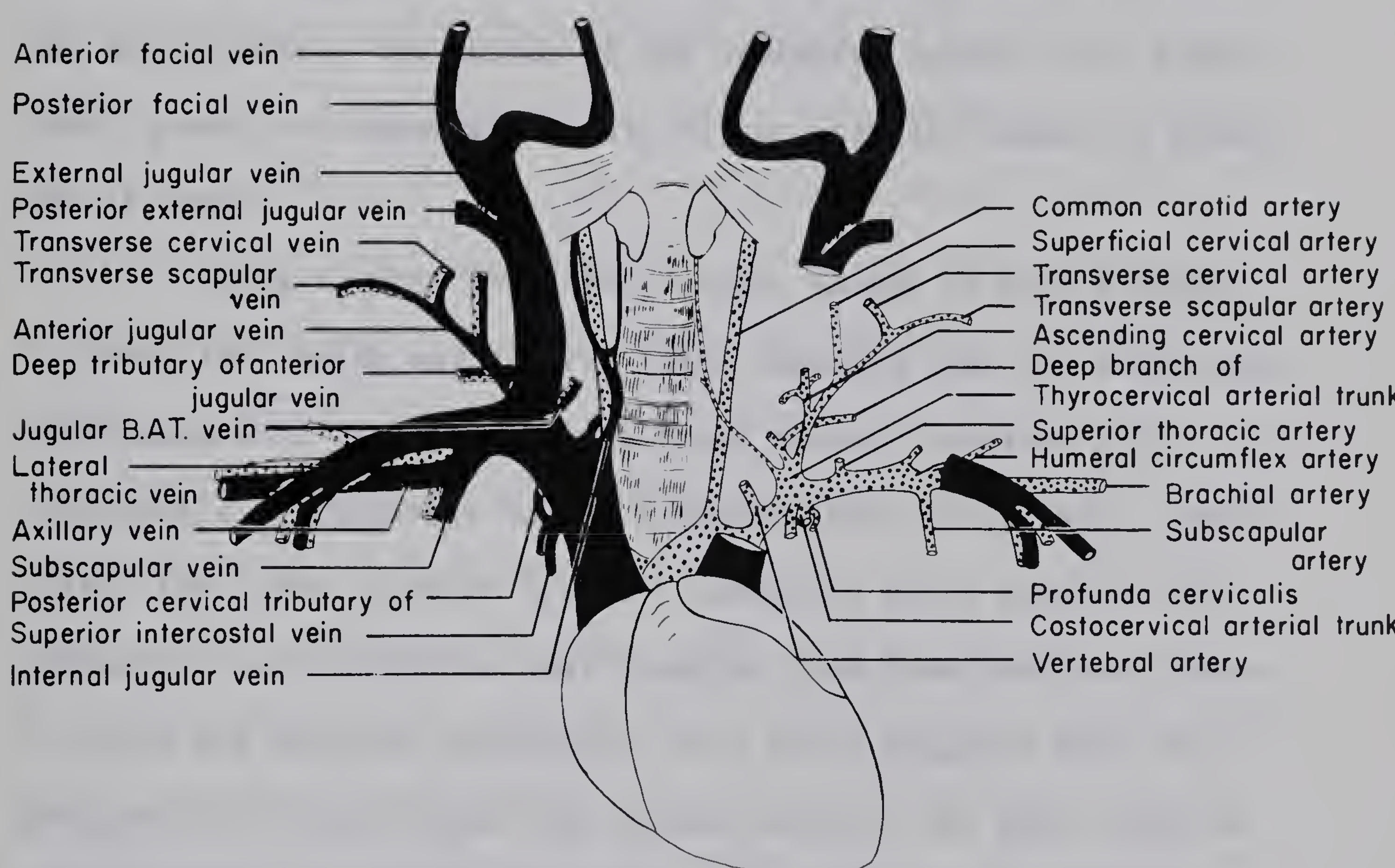

Anterior facial vein
External jugular vein
Transverse cervical vein
Anterior jugular vein
Deep tributary af anterior jugular vein
Lateral tharacic vein
Posterior cervical tributary af superiar intercastal vein
Posteriar facial vein
Pasteriar external jugular vein
Transverse scapular vein
Jugular B.A.T. vein
Internal jugular vein
Vertebral vein
Brachial vein
Subscapular vein
Superior intercostal vein

Fig. 50. Diagram of the relationship between the major anterior arteries and veins of *Peromyscus maniculatus*.


Anterior facial vein
Posterior facial vein
External jugular vein
Posterior external jugular vein
Transverse cervical vein
Transverse scapular vein
Anterior jugular vein
Deep tributary of anterior jugular vein
Jugular B.A.T. vein
Lateral thoracic vein
Axillary vein
Subscapular vein
Posterior cervical tributary of
Superior intercostal vein
Internal jugular vein
Common carotid artery
Superficial cervical artery
Transverse cervical artery
Transverse scapular artery
Ascending cervical artery
Deep branch of
Thyrocervical arterial trunk
Superior thoracic artery
Humeral circumflex artery
Brachial artery
Subscapular artery
Profunda cervicalis
Costocervical arterial trunk
Vertebral artery

DISCUSSION

The general distribution of brown adipose tissue is similar in the bat and deer mouse. It is comparable to that of the laboratory rat (Hammar, 1895; Smith and Roberts, 1964), and presumably to all mammals in which brown fat is found (Auerbach, 1901/02; Johansson, 1959; Cameron and Smith, 1964). The tissue surrounds the more centrally-located blood vessels and adjacent nerves. It overlies the sympathetic chain, cervical plexus, brachial plexus, and approximately two thirds of the vertebral column. The suprarenal glands are embedded in this tissue when the amount of brown fat is large.

Owing to the "absolutely" small amount of heat produced by brown fat, Smith and Roberts (1964) deduced that the functional significance of this tissue as a "heat source" involves its topographic relationship to the aforementioned structures, particularly the blood vascular system. Accepting their proposal of a conductive and convective heat transfer from brown adipose tissue to blood and adjacent structures, this study suggests that the peripherally-cooled blood from distal parts of the body could be warmed before it reaches the heart. The blood of the external and internal jugular veins, transverse cervical, axillary, internal mammary, and azygos veins, as well as the inferior vena cava are subject to heating by conduction and/or convection from the surrounding brown fat. Furthermore, the metabolic activity of brown fat, surrounding the carotid artery, could maintain the temperature of the brain within the required physiological limits when the animal is subjected to unfavourably low environmental temperatures.

Two types of vascular arrangements are associated with the brown fat deposits in the bat and deer mouse. The first, identical in the two species, involves the vascularization of the majority of brown fat deposits; the second, peculiar to the interscapular brown adipose tissue, differs in the bat and deer mouse. Figure 24 shows a typical example of the first type of vascular arrangement. The majority of brown fat deposits are located about segments of major veins and corresponding arteries. These veins do not originate within the brown fat deposit but receive venules from it. They are joined also by major tributaries from elsewhere. Similarly, the main artery does not terminate within the brown fat deposit but supplies branches to it, as well as to other adjacent structures. Therefore, whenever the metabolic heat production of brown adipose tissue is higher than that of adjacent structures, that segment of the vein which passes through the brown fat deposit will receive warm blood from the venules that arise from within the deposit. It will receive cool blood from its peripheral tributaries. The vein will also receive conductive heat from the surrounding brown fat. Arteries and arterioles will be subjected to conductive heat only. This arrangement indicates that not only centrally but also peripherally-situated tissues are subject to metabolic heating by subsequent vascular convection. Since the peripherally-located arteries are not surrounded by brown adipose tissue, there will be a gradual heat loss as the arterial blood flows toward the periphery. Conversely, the returning blood will be warmed gradually by mixing with the warmer blood from brown fat deposits and by increased conductive heat

gain closer to the heart. Such a "gradation system" allows the body core to be the warmest region and, at the same time, prevents damage of central tissues from too sudden a temperature change in peripheral areas.

The vascular arrangements of the interscapular brown adipose tissue in the bat differs from that of other deposits in that the terminal branches of a major vessel, the transverse cervical artery, supply this tissue. The tributaries of the transverse cervical vein, which drain the tissue, originate in it. Methacrylate-injected specimens revealed that the vascularization of this deposit is far more extensive than that of any other deposit encountered. Because of the relatively large fractional mass of interscapular brown fat, the greatest percentage of the total metabolic heat produced by brown adipose tissue during arousal from hibernation will be derived from this deposit. Much of this heat would be conveyed to the heart very quickly via the relatively short course of the transverse cervical vein. Moreover, recent studies (Rauch, unpubl. data) indicate that, in the little brown bat, there is a tenfold increase in the blood flow through brown adipose tissue during arousal from hibernation.

In the deer mouse, the interscapular brown adipose tissue is supplied by the terminal branches of the thoracodorsal artery. The venous shunt system seen here resembles that in the rat. Smith and Roberts (1964) proposed that in the rat heat is transferred, according to the principle of counter-current heat exchange, from the metabolically-warmed blood in the thoracodorsal vein to the slightly cooler blood in the thoracodorsal artery.

The warmer the arterial blood, the greater the metabolic rate and, therefore, the heat production of the interscapular brown fat deposit. To prevent the system from becoming "critical", the venous return can be shunted into the body core via Sulzer's vein. A second alternative, not mentioned by Smith and Roberts, would be a reversal of blood flow in the thoracodorsal vein (Figs. 21, 22, 23, 25, 26) during cold stress. Thus, the returning blood from the deep aspect of the front appendages could be shunted through the interscapular brown fat deposit, providing additional heat transfer to the blood returning to the heart.

The high temperature of brown adipose tissue during arousal from hibernation (Smith and Hock, 1963; Smalley and Dryer, 1963; Hayward and Lyman, 1967), in cold-acclimation (Cameron and Smith, 1964; Smith and Roberts, 1964), and cold-stress (Donhoffer and Szelényi, 1967) implies that, under these conditions, there will be conductive heat transfer from brown fat to adjacent structures. Heat will be conveyed to a considerable portion of the spinal cord from the overlay of the squamo-occipito-cervical and interscapular brown fat deposits. Conductive heat will be received also by the suprarenal glands, sympathetic chain, and the majority of muscles in the thoracic and neck regions. Most, if not all, of these tissues will be subjected also to warming by vascular convection. Therefore, it can be assumed that brown adipose tissue is at least partly responsible for maintaining the homeostasis of these structures in cold stress and presumably for a preferential rewarming of these tissues during arousal from hibernation.

The changes observed in the size of brown fat deposits in the bat and deer mouse coincide with those of other species (Johansson, 1959). Apparently, the amount of brown adipose tissue varies with age, food supply, and season. In marmots *(Marmota monax)*, the tissue is reduced to a minimum mass during rutting time, about four weeks after hibernation ends (Sweet and Hoskins, 1940). Rasmussen (1923), and Hoepke and Nikolaus (1949) claim that the reduction of brown adipose tissue during hibernation is caused by the disappearance of fat vacuoles, shrinkage, and obliteration of the cell structure. On the other hand, von Hanseman (1902) maintains that a reduction in the mass of brown adipose tissue is not associated with cellular destruction. An increase in the relative amount of brown fat in cold-acclimated rats is well documented (Cameron and Smith, 1964; Joel, 1965; Hunt and Hunt, 1967), but quantitative data on the seasonal changes of brown fat in mammals subjected to fluctuating environmental conditions are critically needed. Such information is available only for the shrew (Buchalczyk and Korybska, 1964) and the meadow vole (Didow, 1968). In these animals, the relative amount of brown fat is greatest during the winter and smallest in the summer. Valuable information could be obtained from a long term study of the relative mass and composition of brown adipose tissue in a hibernator and non-hibernator. Since there is suggestive evidence (Cameron and Smith, 1964; Joel, 1965) that white fat is the major source of lipid for the renewal of the brown adipose tissue lipid store, changes in white adipose tissue should be studied simultaneously.

Observations in this study indicated that bats and deer

mice accumulate both white and brown adipose tissue in late summer and autumn. Bats, killed during their arousal from hibernation, had smaller brown fat deposits than their non-hibernating counterparts, probably because the former utilized brown fat during the arousal process. The total absence of white fat in these animals suggests two possibilities. No white fat was present initially. White fat was present; it was mobilized and converted into brown fat during periodic arousal from hibernation, as suggested by Joel (1965); it was mobilized and metabolized elsewhere. The similarity in size of brown fat deposits between warm and cold-acclimated deer mice, and the absence of white fat in the latter, might suggest the utilization of white fat in the replacement of brown fat lipids which were metabolized during the initial cold stress. However, it is equally possible that, during cold stress, white fat lipids were metabolized in some other tissue such as the liver or muscle. As to whether or not white adipose tissue provides a lipid source for the replacement of brown fat lipids is an interesting question which should be investigated. Probably, such a study would involve the use of radio-active tracers.

No quantitative data are available to explain the seasonal changes in the size and vascularization of brown fat deposits in the two species investigated. Increases in cellularity, vascular supply, and total mass of brown fat, and corresponding decreases in the amount of white adipose tissue occur in the rat during cold-acclimation (Cameron and Smith, 1964). Radioautographic studies indicate that, in cold exposure, cell proliferation takes place in "vascular" (endothelial) cells, and in the "precurser"

cells of the extravascular system (Hunt and Hunt, 1967). The former give rise to blood vessels, the latter to brown adipose tissue cells. If cold stress initiates an increase of brown adipose tissue cells in the rat, one might expect to find similar changes in the deer mouse since, phylogenetically, these are closely related species. On the other hand, cold exposure usually evokes an immediate drop in body temperature, and thus, in the metabolism of bats. Therefore, it appears unreasonable that such an energy demanding process as cell proliferation would occur when bats are exposed to cold. It would seem necessary for bats to undergo proliferative changes in their brown adipose tissue prior to seasonal temperature changes. Clearly, a study in this area should be initiated. It would involve small mammals which are subjected to the changing conditions of their environment, and it should include both hibernators and non-hibernators.

The conjecture that the intrathoracic and abdominal brown adipose tissues comprise a single entity might be explained in terms of embryonic development and the changes in brown fat which occur thereafter. During embryonic development, the "Anlagen" or primordia of brown adipose tissue appear in the typical locations where brown fat is found during post natal and adult life (Hammar, 1895). Thus, within the thorax and abdomen, it is found along the major vessels, between the kidneys, and overlying the sympathetic trunk. During cell proliferation, brown adipose tissue cells may be formed throughout the entire region simultaneously. Thus, when the tissue has built up to a maximum, the intrathoracic and abdominal brown adipose tissue forms a

continuous, sheath-like structure. During cell destruction, certain regions may disappear completely, depending on the number of cell layers, stage of depletion of brown fat, age of cells, etc. Therefore, when a minimum amount of brown fat is present, the intrathoracic and abdominal brown adipose tissue appears to be composed of a number of distinct deposits.

In summary, the general disposition of brown adipose tissue is comparable in *Myotis lucifugus lucifugus* and *Peromyscus maniculatus borealis*. Minor interspecific variations in the location of individual deposits were observed in these species. They seem to be related to anatomical differences and may be viewed as a consequence of evolutionary adaptations to different modes of life. This study supports the suggestion of Smith and Roberts (1964) that the importance of brown adipose tissue as a "heat source" involves the close proximity of this tissue to central structures and blood vessels. Thus, conductive and/or convective heat from the metabolism of brown fat may be conveyed rapidly and efficiently to these central structures as well as to peripheral tissues. The importance of such heat transfer mechanisms to the defence of homeothermy during cold stress and to rapid increase in heat content during arousal from hibernation is obvious. It is hoped that this study has contributed to the understanding of such mechanisms by providing a thorough analysis of the anatomical and vascular relations of brown adipose tissue in a hibernator and a non-hibernator. These results may also potentiate further *in vivo* physiological studies of brown adipose tissue; studies that require a precise knowledge of the vascularization of this tissue.

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